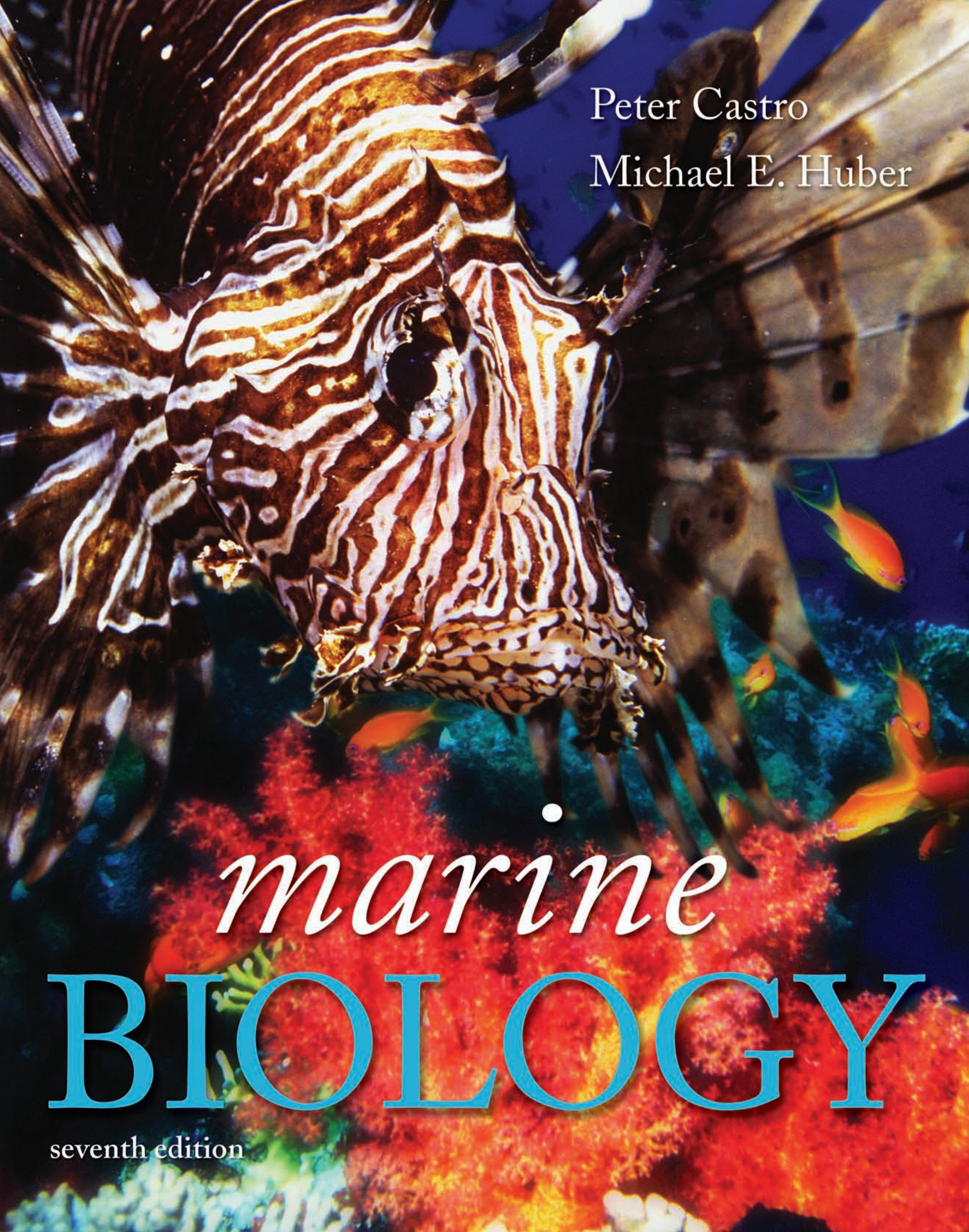

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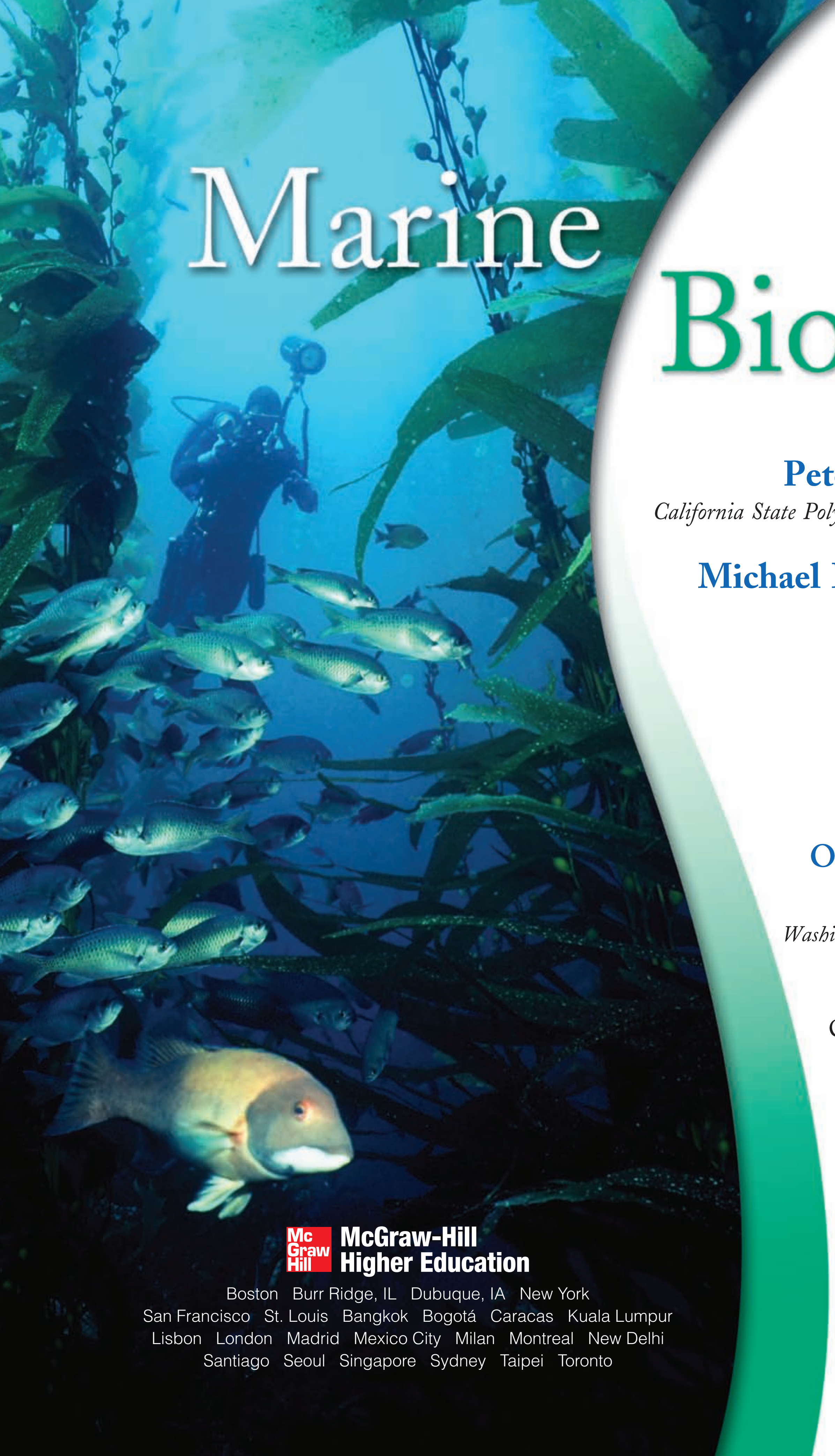

Marine Biology

Seventh Edition

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Dedication

To all future marine biologists

—Peter Castro—

To Kerry, my closest friend, and
to Mason and Erin, watching you
blossom is a never-ending joy.

—Michael Huber—

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About the Authors

Michael Huber, Ph.D.

Michael was immediately fascinated by aquatic organisms when he caught his first trout on an Alaskan lake at age two. His interest in marine biology continued to grow over his ensuing school years, and he went on to obtain B.S. degrees in zoology and oceanography from the University of Washington in Seattle. After spending an Alaskan winter managing a laboratory for the trans-Alaskan oil pipeline project, he entered graduate school at Scripps Institution of Oceanography, at the University of California, San Diego. In 1983 he received his doctorate for research on a group of crabs that live symbiotically with corals. He remained at Scripps as a research biologist, working on such diverse research topics as the genetics and cell biology of unicellular algae and bioluminescence in midwater organisms. In 1988 he moved to the Biology Department at the University of Papua New Guinea, where he had the opportunity to work on some of the world's most spectacular coral reefs and was Head of the University's Motupore Island Research Station. He also became increasingly involved in marine environmental science, especially with regard to reefs, mangroves, seagrass beds, and other tropical systems. This interest continued to grow when he left Papua New Guinea in 1994 to become the Scientific Director of James Cook University's Orpheus Island Research Station on Australia's Great Barrier Reef. In 1998 he became a full-time environmental advisor, providing scientific information and advice on marine environmental issues and the development of conservation programs to international agencies, governments, and private industry. Dr. Huber is the Chair of GESAMP, an international scientific body that advises the United Nations system on marine environmental issues, and he is currently assisting with the establishment of a permanent UN system to assess and report to governments on the state of the global marine environment.

Dr. Huber lives in Brisbane, Australia, with his wife and two children. His hobbies are fishing, diving, swimming, jazz and rock music, reading, and gardening.

Peter Castro, Ph.D.

Peter Castro realized that he had to become a marine biologist during a high school field trip to the coral reefs in his native Puerto Rico. He obtained a B.S. in biology from the University of Puerto Rico, Mayagüez, but left the warm Caribbean for warm Hawaii to obtain a Ph.D. in marine zoology from the University of Hawaii, Manoa. His first experience with cold water was a year of post-doctoral research at Hopkins Marine Station of Stanford University in Monterey Bay, California. He is currently professor at California State Polytechnic University, Pomona. He also holds a B.A. in history and art history from his home institution, something that took him eighteen years to accomplish as a part-time student. He is fluent in five languages and taught marine biology (in English and Spanish) as a Fulbright Scholar at Odessa State University in the former Soviet Union. His research specialty is the biology of crustaceans symbiotic with reef corals and other invertebrates, a research that has taken him anywhere where the water is warm enough to dive. He has also been doing research for almost the last two decades on the systematics of deep-water crabs, mostly, of all places, in Paris, France. His research has also taken him in the last couple of years to Singapore, London, Hawai'i, the Seychelles and Vietnam.

Preface

The beauty, mystery, and power of the sea fascinate people all over the world, including, of course, students enrolled in undergraduate marine biology courses. For many students taking marine biology is the natural expression of an interest in marine life that began by visiting the shore, scuba diving, recreational fishing, aquarium keeping, or viewing one of the many superb television documentaries about the ocean. Many students are also concerned about the increasing impacts of humans on marine ecosystems. ***Marine Biology*, seventh edition,** was written to reinforce and enhance our readers' enchantment with marine life while providing a rigorous introduction to marine biology as a science.

Marine Biology is used by high school, undergraduate, graduate, and adult-education students, as well as by interested laypersons not enrolled in formal courses. We are gratified that even many professional marine biologists find the book useful. While keeping this range of users in mind, we have written the text primarily to meet the needs of lower-division, non-science majors at colleges and universities. For many of these students, marine biology will be their only tertiary science course, often taken to satisfy a general education requirement. We have therefore been careful to provide solid basic science coverage, including some principles of the scientific method, the physical sciences, and basic biology. Our aim has been to integrate this basic science content with a stimulating, up-to-date overview of marine biology. We hope this approach demonstrates the relevance of the physical sciences to biology and makes all sciences less intimidating. To this end, we use an informal writing style that emphasizes an understanding of concepts over rigorous detail and terminology.

We recognize that general science content is not a requirement for all marine biology courses, either because the course is not intended to satisfy general education requirements or because students already have a background in science. To balance the needs of instructors teaching courses with and without prerequisites in biology or other sciences, we have designed the book to provide as much flexibility as possible in the use of the basic science material, the order in which topics are presented, and overall emphasis and approach. We have tried to meet the needs and expectations of a wide variety of students, from the scuba-diving philosophy major to the biology major considering a marine science career. We hope a variety of readers other than university students also find the book useful and enjoyable.

Four major themes run through ***Marine Biology.*** One is the abovementioned coverage of basic science applied to the marine environment. Another is an emphasis on the organisms themselves, and their vast diversity not only in taxonomic terms but also in structure, function, and ecology. A third theme is an ecosystem approach that integrates this organismal diversity with the challenges imposed by the surrounding environment, both physical and biological. A final theme that, for better or worse, becomes increasingly relevant with each passing year is the interaction of humans with the marine environment.

***Marine Biology*, seventh edition,** adopts a global perspective to emphasize that the world's oceans and seas are an integrated system that cannot be understood by looking in any one person's own backyard. For many students this is a new perspective. One aspect of our global approach is the deliberate inclusion of examples from many different regions and ecosystems so that as many students as possible, not just in North America but around the world, will find something relevant to their local areas or places they have visited. We hope this will stimulate them to think about the many relationships between their own shores and the one world ocean that so greatly influences our lives.

CHANGES IN THE SEVENTH EDITION

A major new feature of the seventh edition is a "Special Report" highlighting several key aspects of global change, including climate change, ocean acidification, the cascade of reactive nitrogen into the global environment, and stratospheric ozone depletion. These topics are by no means new to ***Marine Biology*** but, with the torrent of recent research demonstrating the ubiquity and magnitude of the human footprint on earth's ecosystem processes, we felt it was important to delve more deeply into these issues than in previous editions, in a more integrated way. We are eager to hear from instructors about this new section and hope to highlight other aspects of global change—for example, changing sediment fluxes and how overfishing is altering food webs, in future editions. Most of all we hope that in future editions we will be able to highlight more success stories about humanity's progress toward a sustainable existence on our home planet.

We have "expanded" the coverage of organismal biology in Part 2, at the suggestion of a number of instructors, to provide more extensive information about the diversity, form, and function of marine life. Some examples of this enhanced material are

- Illustrated tables at the end of each chapter that provide a consolidated review of major taxonomic groups and their characteristics
- Expanded coverage of marine viruses in a new section in Chapter 5
- New or improved figures on the anatomy of cnidarians, hydroids, polychaetes, squids, sea urchins, and tunicates, as well as on the life cycles of hydroids and sponges

Instructors have responded positively to the "Eye on Science" boxes—brief vignettes of major research programs or individual research projects—introduced in the sixth edition of ***Marine Biology***, and we have retained this feature in the seventh edition to highlight new research and update the progress of ongoing initiatives.

In addition to these and other changes we have, as in every edition, revised the text and illustrations, corrected and updated facts and figures, and adjusted the balance and organization of material in response to new research and the suggestions of reviewers, whose inputs we greatly appreciate. As always we have tried to improve the illustrations and photographs and make the design more visually inviting, in the seventh edition emphasizing the central role of an evolutionary perspective in biology. We are deeply appreciative of the both the efforts and dedication of doday's marine biologists who teach the subject and of the hard work and aspirations of the students who are tomorrow's citizens and in some cases marine biologists. We sincerely hope that ***Marine Biology***, seventh edition, will continue to support both teacher and student.

ORGANIZATION

Marine Biology is organized into four parts. **Part 1** (Chapters 1 through 4) introduces students to marine biology and the basic sciences that underpin it. Chapter 1 describes the history of marine biology. It also explains the fundamentals of the scientific method. This feature emphasizes that science is a process, an ongoing human endeavor. We think it critical that students understand how and why science works and that science has limitations and that there is still much to be learned. Chapters 2 and 3 are a basic introduction to marine geology, physics, and chemistry. ***Marine Biology*** includes more information on these subjects, and places greater stress on their importance to understanding marine ecosystems, than other texts but we have kept Chapters 2 and 3 as short as possible and cover many abiotic aspects of the marine environment in the chapters where they are most relevant to the biology. Wave refraction, for example, is described in conjunction with intertidal communities (Chapter 11) and estuarine circulation is discussed as part of the ecology of estuaries (Chapter 12). This approach emphasizes the importance of the physical and chemical environment to the organisms of the sea throughout the book. At the same time, it provides flexibility for instructors to make best use of the material in light of general education requirements, course prerequisites, and students' backgrounds. Chapter 4, "Fundamentals of Biology," briefly reviews some essential biological concepts. In covering basic biology we have tried to balance the needs of a spectrum of students ranging from those with no prior university-level instruction to those who have taken a number of biology courses. Depending on the level of their students, instructors may choose to cover Chapter 4 in class, assign it as review reading, or omit it and rely on the in-text glossary entries in later chapters to remind students of the definitions of key terms.

Part 2 (Chapters 5 through 9) surveys the diversity of marine life from the perspective of organismal biology. As in Part 1, we provide introductory information that is reviewed and expanded upon in later chapters. In discussing the various taxa we emphasize functional morphology, ecological and physiological adaptations, and economic importance or other significance to humanity. Classification and phylogeny are not stressed, though we do present cladograms illustrating widely accepted phylogenetic schemes for invertebrates and vertebrates. As in the rest of the book we have selected organisms from around the world for illustration in photographs, line drawings, and color paintings, but organisms from the coasts of North America are emphasized. Organisms are referred to by their most widely accepted common names. One or two common or important genera are noted in parentheses the first time a group is mentioned in a chapter, but we have not attempted to provide comprehensive lists of genera. Nomenclature follows for the most part the FAO Species Catalog and Species Identification Guides for groups covered by these references.

Part 3 of the book (Chapters 10 through 16) presents an ecological tour of the major environments of the world ocean, commencing with an introduction to some fundamental principles of marine ecology in Chapter 10. As for Chapter 4, important concepts presented here are reviewed elsewhere in the in-text glossary boxes. The remaining six chapters of Part 3 proceed from nearshore to offshore and from shallow to deep water, describing the physical characteristics of each environment and the adaptations and interactions of the organisms that live there. This admittedly arbitrary sequence follows the teaching sequence of the greatest number of our reviewers, but the chapters are designed so that they can be covered in any sequence according to instructors' preferences and needs. Most chapters include generalized food webs with standardized color coding to indicate the nature of the trophic relationships.

Finally, **Part 4** looks at the many ways in which humans interact with the world ocean: our use of and impact on the marine environment and the influence of the ocean on the human experience. The section presents an up-to-date, comprehensive view of issues and concerns shared by many students. The chapter on resource utilization (Chapter 17) looks not only at traditional uses, such as fisheries and mariculture, but also at more modern aspects, such as the pharmacological use of marine natural products and the application of genetic engineering to mariculture. Chapter 18 discusses human-induced degradation of the marine environment, balanced by an examination of marine conservation and habitat restoration. The book closes with an essay on the interactions between the ocean and the human culture (Chapter 19) that we hope will stimulate students to reflect on the past and future significance of the world ocean to all our lives.

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Bill Ober and Claire Garrison have again done a wonderful job of bringing new life to the illustrations. We are delighted by the new design by Jamie O'Neal. We also thank the many contributors of photographs that add so much to the book, especially A. Charles Arneson, who has provided many excellent photos, and appreciate the diligent efforts of LouAnn Wilson in locating new photos. We are grateful to the editorial and production staff at McGraw-Hill Publishers, particularly Patrick Reidy, Executive Editor, Debra Henricks, Developmental Editor, Joyce Watters, Project Manager, and Deb DeBord, copy editor, for their patience, support, and efficiency in managing an enormous amount of detail. Most of all we thank the students, friends, colleagues, former teachers, and reviewers who answered questions, pointed out errors, and made suggestions that have greatly improved the

book. We take full credit, however, for any errors or shortcomings that remain.

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REVIEWERS

The following people reviewed the sixth edition and have provided useful commentary for preparation of the seventh edition:

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Christopher Brown, *Florida International University*
Edward J. Carpenter, *San Francisco State University*
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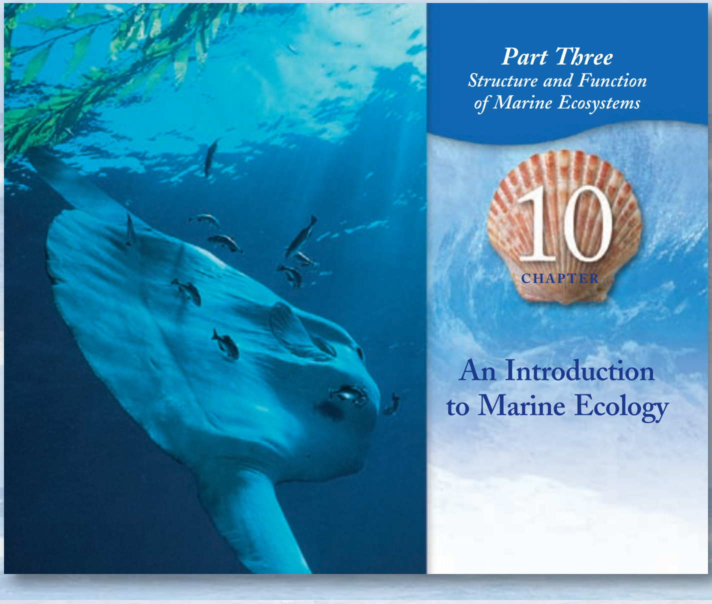
The Marine Biology
Learning System

Chapters

Are organized into four parts and written as short, readily absorbed units to increase instructor flexibility in selecting topics.



Part Three
Structure and Function of Marine Ecosystems

10 CHAPTER

An Introduction to Marine Ecology

11
CHAPTER
Rocky intertidal, Mo
12
CHAPTER
Estuary
Salt marsh and mudf
13
CHAPTER
Subtidal zone
Continental shelf

Life on the Continental Shelf

Ecklonia kelp forest, New Zealand.

The submerged edge of the continents, the **continental shelf,** was once considered the beginning of the unknown blue sea. But when the shelf came under scrutiny during the 1800s, the unknown began to give up its secrets. We have learned even more because the use of scuba and underwater habitats has allowed firsthand study and observation (Fig. 13.1). Biologically, the shelf is the richest part of the ocean. It includes the world's most important fishing grounds, which yield about 90% of the total global catch. Oil and minerals have been found on the shelf, and nations have extended their international borders to protect their newfound, or yet-to-be found, resources. The continental shelf, being close to shore, is also profoundly affected by pollution and other activities of humans on land.

This chapter looks at life on the continental shelf, paying particular attention to the bottom organisms. Life in the water column above the shelf is discussed in Chapter 15, and the shelf's fisheries in Chapter 17. Coral reefs, many of which are found on the shelf, are covered separately in Chapter 14.

PHYSICAL CHARACTERISTICS OF THE SUBTIDAL ENVIRONMENT

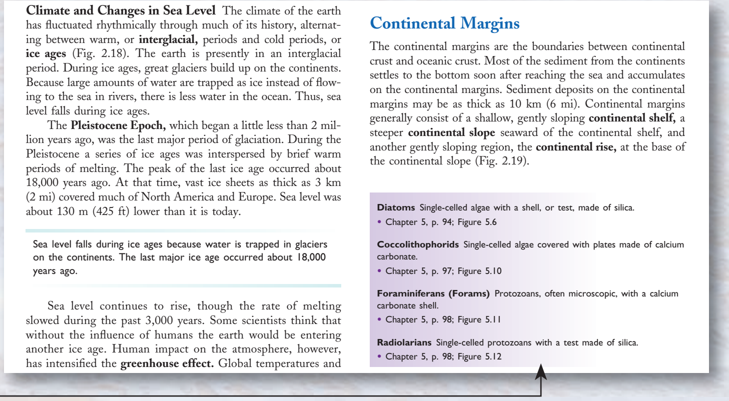
The part of the continental shelf that is never exposed at low tide constitutes the **subtidal zone** of the marine environment. The subtidal zone, which is sometimes called the **sublittoral zone,** extends from the low tide level on shore to the **shelf break,** the outer edge of the continental shelf (see Fig. 10.12). The depth

Key Concept Summaries

Highlight the most important terms and ideas presented in preceding paragraphs.

In-Text Glossary

Briefly explains key terms and concepts from other chapters. Chapter and page references point students to more detailed information. The extensive **glossary** in the back of the book provides complete definitions and often refers to illustrations or other key terms that help explain a concept.



Climate and Changes in Sea Level The climate of the earth has fluctuated rhythmically through much of its history, alternating between warm, or **interglacial,** periods and cold periods, or **ice ages** (Fig. 2.18). The earth is presently in an interglacial period. During ice ages, great glaciers build up on the continents. Because large amounts of water are trapped as ice instead of flowing to the sea in rivers, there is less water in the ocean. Thus, sea level falls during ice ages.

The **Pleistocene Epoch,** which began a little less than 2 million years ago, was the last major period of glaciation. During the Pleistocene a series of ice ages was interspersed by brief warm periods of melting. The peak of the last ice age occurred about 18,000 years ago. At that time, vast ice sheets as thick as 3 km (2 mi) covered much of North America and Europe. Sea level was about 130 m (425 ft) lower than it is today.

Sea level falls during ice ages because water is trapped in glaciers on the continents. The last major ice age occurred about 18,000 years ago.

Sea level continues to rise, though the rate of melting slowed during the past 3,000 years. Some scientists think that without the influence of humans the earth would be entering another ice age. Human impact on the atmosphere, however, has intensified the **greenhouse effect.** Global temperatures and

Continental Margins

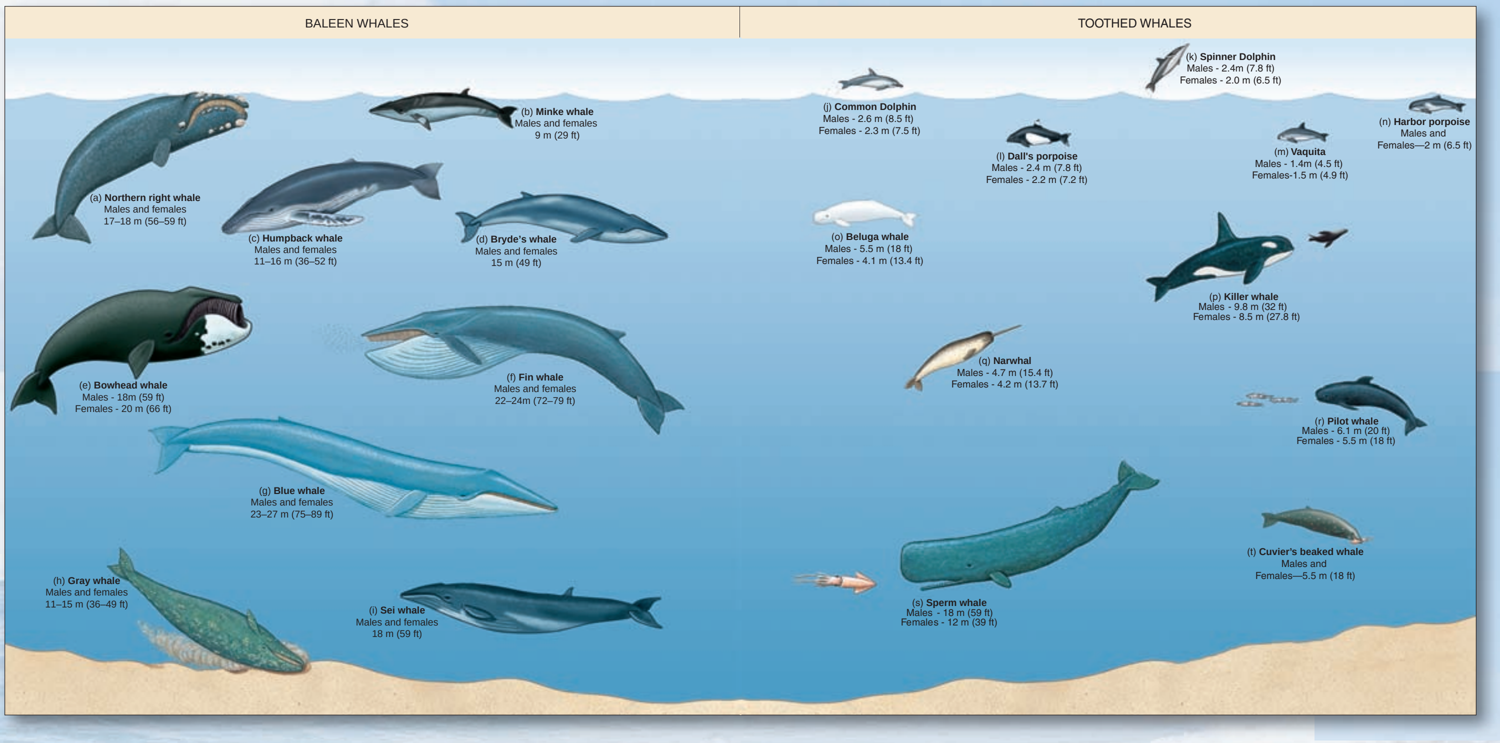
The continental margins are the boundaries between continental crust and oceanic crust. Most of the sediment from the continents settles to the bottom soon after reaching the sea and accumulates on the continental margins. Sediment deposits on the continental margins may be as thick as 10 km (6 mi). Continental margins generally consist of a shallow, gently sloping **continental shelf,** a steeper **continental slope** seaward of the continental shelf, and another gently sloping region, the **continental rise,** at the base of the continental slope (Fig. 2.19).

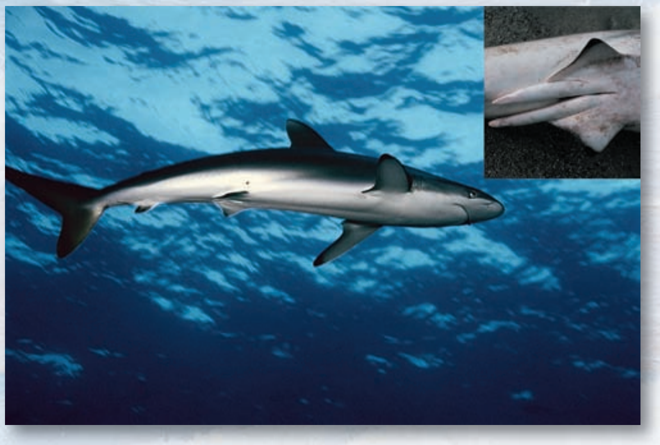
Diatoms Single-celled algae with a shell, or test, made of silica.
- Chapter 5, p. 94; Figure 5.6

Coccolithophorids Single-celled algae covered with plates made of calcium carbonate.
- Chapter 5, p. 97; Figure 5.10

Foraminiferans (Forams) Protozoans, often microscopic, with a calcium carbonate shell.
- Chapter 5, p. 98; Figure 5.11

Radiolarians Single-celled protozoans with a test made of silica.
- Chapter 5, p. 98; Figure 5.12


BALEEN WHALES
TOOTHED WHALES
(a) Northern right whale
Males and females
17–18 m (56–59 ft)
(b) Minke whale
Males and females
9 m (29 ft)
(c) Humpback whale
Males and females
11–16 m (36–52 ft)
(d) Bryde's whale
Males and females
15 m (49 ft)
(e) Bowhead whale
Males - 18m (59 ft)
Females - 20 m (66 ft)
(f) Fin whale
Males and females
22–24m (72–79 ft)
(g) Blue whale
Males and females
23–27 m (75–89 ft)
(h) Gray whale
Males and females
11–15 m (36–49 ft)
(i) Sei whale
Males and females
18 m (59 ft)
(j) Common Dolphin
Males - 2.6 m (8.5 ft)
Females - 2.3 m (7.5 ft)
(k) Spinner Dolphin
Males - 2.4m (7.8 ft)
Females - 2.0 m (6.5 ft)
(l) Dall's porpoise
Males - 2.4 m (7.8 ft)
Females - 2.2 m (7.2 ft)
(m) Vaquita
Males - 1.4m (4.5 ft)
Females-1.5 m (4.9 ft)
(n) Harbor porpoise
Males and
Females—2 m (6.5 ft)
(o) Beluga whale
Males - 5.5 m (18 ft)
Females - 4.1 m (13.4 ft)
(p) Killer whale
Males - 9.8 m (32 ft)
Females - 8.5 m (27.8 ft)
(q) Narwhal
Males - 4.7 m (15.4 ft)
Females - 4.2 m (13.7 ft)
(r) Pilot whale
Males - 6.1 m (20 ft)
Females - 5.5 m (18 ft)
(s) Sperm whale
Males - 18 m (59 ft)
Females - 12 m (39 ft)
(t) Cuvier's beaked whale
Males and
Females—5.5 m (18 ft)



Illustrations and photographs have been carefully designed and selected to complement and reinforce the text. The seventh edition contains many new illustrations and photographs.

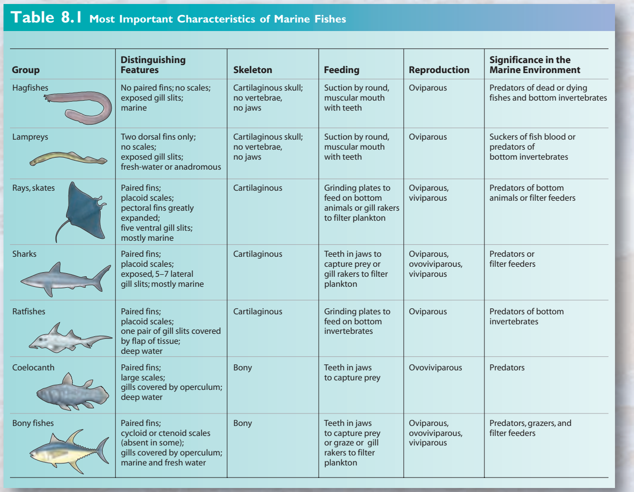
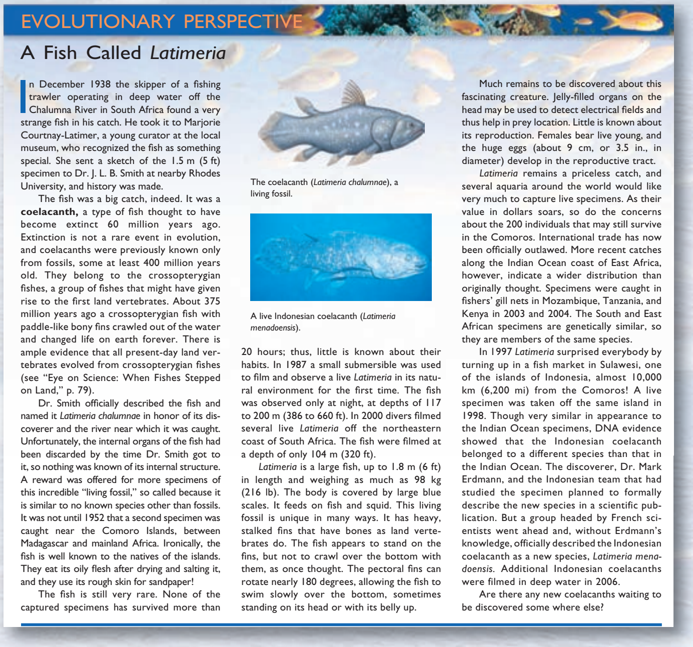


Table 8.1 **Most Important Characteristics of Marine Fishes**

Group	Distinguishing Features	Skeleton	Feeding	Reproduction	Significance in the Marine Environment
Hagfishes	No paired fins; no scales; exposed gill slits; marine	Cartilaginous skull; no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Predators of dead or dying fishes and bottom invertebrates
Lampreys	Two dorsal fins only; no scales; exposed gill slits; fresh-water or anadromous	Cartilaginous skull; no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Suckers of fish blood or predators of bottom invertebrates
Rays, skates	Paired fins; placoid scales; pectoral fins greatly expanded; five ventral gill slits; mostly marine	Cartilaginous	Grinding plates to feed on bottom animals or gill rakers to filter plankton	Oviparous, viviparous	Predators of bottom animals or filter feeders
Sharks	Paired fins; placoid scales; exposed, 5–7 lateral gill slits; mostly marine	Cartilaginous	Teeth in jaws to capture prey or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators or filter feeders
Ratfishes	Paired fins; placoid scales; one pair of gill slits covered by flap of tissue; deep water	Cartilaginous	Grinding plates to feed on bottom invertebrates	Oviparous	Predators of bottom invertebrates
Coelocanth	Paired fins; large scales; gills covered by operculum; deep water	Bony	Teeth in jaws to capture prey	Ovoviviparous	Predators
Bony fishes	Paired fins; cycloid or ctenoid scales (absent in some); gills covered by operculum; marine and fresh water	Bony	Teeth in jaws to capture prey or graze or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators, grazers, and filter feeders



EVOLUTIONARY PERSPECTIVE

A Fish Called *Latimeria*

In December 1938 the skipper of a fishing trawler operating in deep water off the Chalumna River in South Africa found a very strange fish in his catch. He took it to Marjorie Courtnay-Latimer, a young curator at the local museum, who recognized the fish as something special. She sent a sketch of the 1.5 m (5 ft) specimen to Dr. J. L. B. Smith at nearby Rhodes University, and history was made.

The fish was a big catch, indeed. It was a **coelacanth,** a type of fish thought to have become extinct 60 million years ago. Extinction is not a rare event in evolution, and coelacanths were previously known only from fossils, some at least 400 million years old. They belong to the crossopterygian fishes, a group of fishes that might have given rise to the first land vertebrates. About 375 million years ago a crossopterygian fish with paddle-like bony fins crawled out of the water and changed life on earth forever. There is ample evidence that all present-day land vertebrates evolved from crossopterygian fishes (see "Eye on Science: When Fishes Stepped on Land," p. 79).

Dr. Smith officially described the fish and named it *Latimeria chalumnae* in honor of its discoverer and the river near which it was caught. Unfortunately, the internal organs of the fish had been discarded by the time Dr. Smith got to it, so nothing was known of its internal structure. A reward was offered for more specimens of this incredible "living fossil," so called because it is similar to no known species other than fossils. It was not until 1952 that a second specimen was caught near the Comoro Islands, between Madagascar and mainland Africa. Ironically, the fish is well known to the natives of the islands. They eat its oily flesh after drying and salting it, and they use its rough skin for sandpaper!

The fish is still very rare. None of the captured specimens has survived more than 20 hours; thus, little is known about their habits. In 1987 a small submersible was used to film and observe a live *Latimeria* in its natural environment for the first time. The fish was observed only at night, at depths of 117 to 200 m (386 to 660 ft). In 2000 divers filmed several live *Latimeria* off the northeastern coast of South Africa. The fish were filmed at a depth of only 104 m (320 ft).

The coelacanth (*Latimeria chalumnae*), a living fossil.

A live Indonesian coelacanth (*Latimeria menadoensis*).

Latimeria is a large fish, up to 1.8 m (6 ft) in length and weighing as much as 98 kg (216 lb). The body is covered by large blue scales. It feeds on fish and squid. This living fossil is unique in many ways. It has heavy, stalked fins that have bones as land vertebrates do. The fish appears to stand on the fins, but not to crawl over the bottom with them, as once thought. The pectoral fins can rotate nearly 180 degrees, allowing the fish to swim slowly over the bottom, sometimes standing on its head or with its belly up.

Much remains to be discovered about this fascinating creature. Jelly-filled organs on the head may be used to detect electrical fields and thus help in prey location. Little is known about its reproduction. Females bear live young, and the huge eggs (about 9 cm, or 3.5 in., in diameter) develop in the reproductive tract.

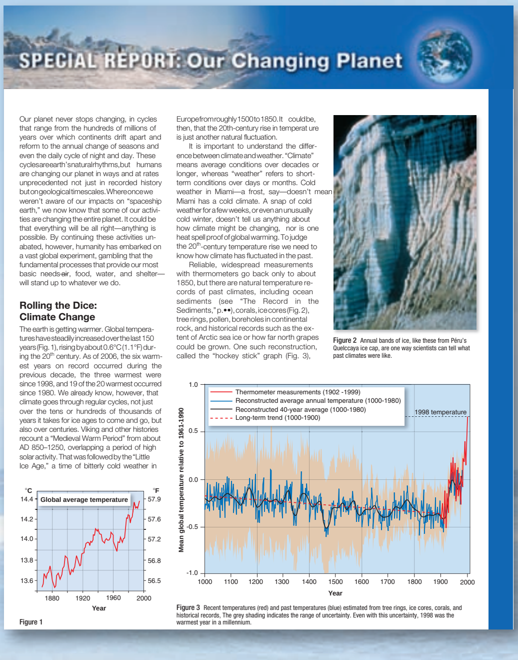
Latimeria remains a priceless catch, and several aquaria around the world would like very much to capture live specimens. As their value in dollars soars, so do the concerns about the 200 individuals that may still survive in the Comoros. International trade has now been officially outlawed. More recent catches along the Indian Ocean coast of East Africa, however, indicate a wider distribution than originally thought. Specimens were caught in fishers' gill nets in Mozambique, Tanzania, and Kenya in 2003 and 2004. The South and East African specimens are genetically similar, so they are members of the same species.

In 1997 *Latimeria* surprised everybody by turning up in a fish market in Sulawesi, one of the islands of Indonesia, almost 10,000 km (6,200 mi) from the Comoros! A live specimen was taken off the same island in 1998. Though very similar in appearance to the Indian Ocean specimens, DNA evidence showed that the Indonesian coelacanth belonged to a different species than that in the Indian Ocean. The discoverer, Dr. Mark Erdmann, and the Indonesian team that had studied the specimen planned to formally describe the new species in a scientific publication. But a group headed by French scientists went ahead and, without Erdmann's knowledge, officially described the Indonesian coelacanth as a new species, *Latimeria menadoensis*. Additional Indonesian coelacanths were filmed in deep water in 2006.

Are there any new coelacanths waiting to be discovered some where else?

Boxed Essays present interesting supplemental information on varied subjects such as deep-water coral communities, tsunamis, and red tides. A number of boxes have been highlighted as "Evolutionary Perspective" boxes to emphasize the central role of an evolutionary perspective in biology.

New! Illustrated tables at the end of each chapter in Part Two provide a consolidated review of major taxonomic groups and their characteristics.



SPECIAL REPORT: Our Changing Planet

Our planet never stops changing, in cycles that range from the hundreds of millions of years over which continents drift apart and reform to the annual change of seasons and even the daily cycle of night and day. These cycles are earth's natural rhythms, but humans are changing our planet in ways and at rates unprecedented not just in recorded history but on geological timescales. Where once we weren't aware of our impacts on "spaceship earth," we now know that some of our activities are changing the entire planet. It could be that everything will be all right—anything is possible. By continuing these activities unabated, however, humanity has embarked on a vast global experiment, gambling that the fundamental processes that provide our most basic needs~~air~~, food, water, and shelter—will stand up to whatever we do.

Rolling the Dice: Climate Change

The earth is getting warmer. Global temperatures have steadily increased over the last 150 years (Fig. 1), rising by about 0.6°C (1.1°F) during the 20th century. As of 2006, the six warmest years on record occurred during the previous decade, the three warmest were since 1998, and 19 of the 20 warmest occurred since 1980. We already know, however, that climate goes through regular cycles, not just over the tens or hundreds of thousands of years it takes for ice ages to come and go, but also over centuries. Viking and other histories recount a "Medieval Warm Period" from about AD 850–1250, overlapping a period of high solar activity. That was followed by the "Little Ice Age," a time of bitterly cold weather in Europe from roughly 1500 to 1850. It could be, then, that the 20th-century rise in temperat ure is just another natural fluctuation.

It is important to understand the difference between climate and weather. "Climate" means average conditions over decades or longer, whereas "weather" refers to short-term conditions over days or months. Cold weather in Miami—a frost, say—doesn't mean Miami has a cold climate. A snap of cold weather for a few weeks, or even an unusually cold winter, doesn't tell us anything about how climate might be changing, nor is one heat spell proof of global warming. To judge the 20th-century temperature rise we need to know how climate has fluctuated in the past.

Reliable, widespread measurements with thermometers go back only to about 1850, but there are natural temperature records of past climates, including ocean sediments (see "The Record in the Sediments," p.••), corals, ice cores (Fig. 2), tree rings, pollen, boreholes in continental rock, and historical records such as the extent of Arctic sea ice or how far north grapes could be grown. One such reconstruction, called the "hockey stick" graph (Fig. 3),

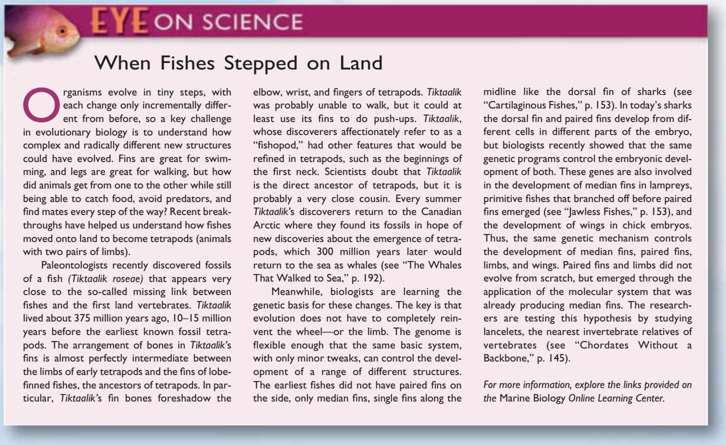
Figure 2 Annual bands of ice, like these from Péru's Quelccaya ice cap, are one way scientists can tell what past climates were like.

°C
°F
Global average temperature
Year
Thermometer measurements (1902 -1999)
Reconstructed average annual temperature (1000-1980)
Reconstructed 40-year average (1000-1980)
Long-term trend (1000-1900)
1998 temperature
Mean global temperature relative to 1961-1990
Year

Figure 1

Figure 3 Recent temperatures (red) and past temperatures (blue) estimated from tree rings, ice cores, corals, and historical records, The grey shading indicates the range of uncertainty. Even with this uncertainty, 1998 was the warmest year in a millennium.

New Feature! A major highlight of the seventh edition is a new insert located after Chapter 10, ***Special Report: Our Changing Planet.*** This current and informative insert highlights several key aspects of global change, including global warming, ocean acidification, eutrophication, hypoxic zones, and stratospheric ozone depletion.



EYE ON SCIENCE

When Fishes Stepped on Land

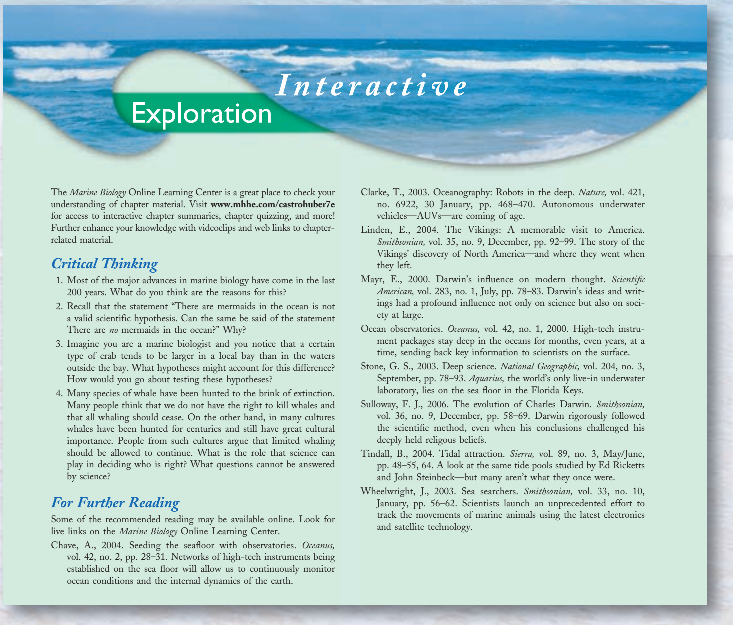
Organisms evolve in tiny steps, with each change only incrementally different from before, so a key challenge in evolutionary biology is to understand how complex and radically different new structures could have evolved. Fins are great for swimming, and legs are great for walking, but how did animals get from one to the other while still being able to catch food, avoid predators, and find mates every step of the way? Recent breakthroughs have helped us understand how fishes moved onto land to become tetrapods (animals with two pairs of limbs).

Paleontologists recently discovered fossils of a fish *(Tiktaalik roseae)* that appears very close to the so-called missing link between fishes and the first land vertebrates. *Tiktaalik* lived about 375 million years ago, 10–15 million years before the earliest known fossil tetrapods. The arrangement of bones in *Tiktaalik's* fins is almost perfectly intermediate between the limbs of early tetrapods and the fins of lobe-finned fishes, the ancestors of tetrapods. In particular, *Tiktaalik's* fin bones foreshadow the elbow, wrist, and fingers of tetrapods. *Tiktaalik* was probably unable to walk, but it could at least use its fins to do push-ups. *Tiktaalik*, whose discoverers affectionately refer to as a "fishopod," had other features that would be refined in tetrapods, such as the beginnings of the first neck. Scientists doubt that *Tiktaalik* is the direct ancestor of tetrapods, but it is probably a very close cousin. Every summer *Tiktaalik's* discoverers return to the Canadian Arctic where they found its fossils in hope of new discoveries about the emergence of tetrapods, which 300 million years later would return to the sea as whales (see "The Whales That Walked to Sea," p. 192).

Meanwhile, biologists are learning the genetic basis for these changes. The key is that evolution does not have to completely reinvent the wheel—or the limb. The genome is flexible enough that the same basic system, with only minor tweaks, can control the development of a range of different structures. The earliest fishes did not have paired fins on the side, only median fins, single fins along the midline like the dorsal fin of sharks (see "Cartilaginous Fishes," p. 153). In today's sharks the dorsal fin and paired fins develop from different cells in different parts of the embryo, but biologists recently showed that the same genetic programs control the embryonic development of both. These genes are also involved in the development of median fins in lampreys, primitive fishes that branched off before paired fins emerged (see "Jawless Fishes," p. 153), and the development of wings in chick embryos. Thus, the same genetic mechanism controls the development of median fins, paired fins, limbs, and wings. Paired fins and limbs did not evolve from scratch, but emerged through the application of the molecular system that was already producing median fins. The researchers are testing this hypothesis by studying lancelets, the nearest invertebrate relatives of vertebrates (see "Chordates Without a Backbone," p. 145).

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

Eye on Science boxes reflect current scientific research and technology in the field of marine biology. Sample topics include the evolution of tetrapods, seagrass wasting disease, the Reef Check program, and the Gulf of Mexico hypoxic zone.



Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Most of the major advances in marine biology have come in the last 200 years. What do you think are the reasons for this?
2. Recall that the statement "There are mermaids in the ocean is not a valid scientific hypothesis. Can the same be said of the statement There are *no* mermaids in the ocean?" Why?
3. Imagine you are a marine biologist and you notice that a certain type of crab tends to be larger in a local bay than in the waters outside the bay. What hypotheses might account for this difference? How would you go about testing these hypotheses?
4. Many species of whale have been hunted to the brink of extinction. Many people think that we do not have the right to kill whales and that all whaling should cease. On the other hand, in many cultures whales have been hunted for centuries and still have great cultural importance. People from such cultures argue that limited whaling should be allowed to continue. What is the role that science can play in deciding who is right? What questions cannot be answered by science?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

Chave, A., 2004. Seeding the seafloor with observatories. *Oceanus,* vol. 42, no. 2, pp. 28–31. Networks of high-tech instruments being established on the sea floor will allow us to continuously monitor ocean conditions and the internal dynamics of the earth.

Clarke, T., 2003. Oceanography: Robots in the deep. *Nature,* vol. 421, no. 6922, 30 January, pp. 468–470. Autonomous underwater vehicles—AUVs—are coming of age.

Linden, E., 2004. The Vikings: A memorable visit to America. *Smithsonian,* vol. 35, no. 9, December, pp. 92–99. The story of the Vikings' discovery of North America—and where they went when they left.

Mayr, E., 2000. Darwin's influence on modern thought. *Scientific American,* vol. 283, no. 1, July, pp. 78–83. Darwin's ideas and writings had a profound influence not only on science but also on society at large.

Ocean observatories. *Oceanus,* vol. 42, no. 1, 2000. High-tech instrument packages stay deep in the oceans for months, even years, at a time, sending back key information to scientists on the surface.

Stone, G. S., 2003. Deep science. *National Geographic,* vol. 204, no. 3, September, pp. 78–93. *Aquarius,* the world's only live-in underwater laboratory, lies on the sea floor in the Florida Keys.

Sulloway, F. J., 2006. The evolution of Charles Darwin. *Smithsonian,* vol. 36, no. 9, December, pp. 58–69. Darwin rigorously followed the scientific method, even when his conclusions challenged his deeply held religous beliefs.

Tindall, B., 2004. Tidal attraction. *Sierra,* vol. 89, no. 3, May/June, pp. 48–55, 64. A look at the same tide pools studied by Ed Ricketts and John Steinbeck—but many aren't what they once were.

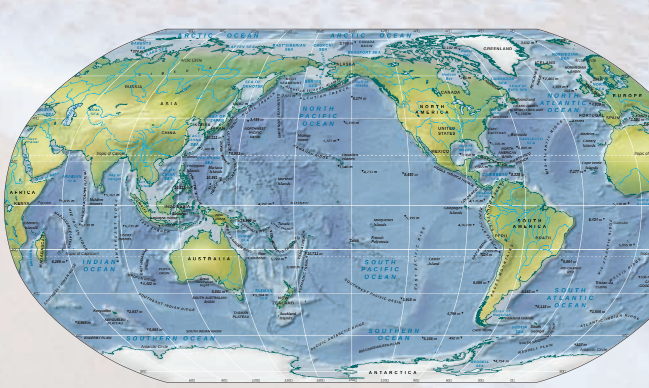
Wheelwright, J., 2003. Sea searchers. *Smithsonian,* vol. 33, no. 10, January, pp. 56–62. Scientists launch an unprecedented effort to track the movements of marine animals using the latest electronics and satellite technology.

Each chapter ends with an **Interactive Exploration** to be used in conjunction with the ***Marine Biology Online Learning Center.*** Students are encouraged to visit **www.mhhe.com/castrohuber7e** for access to chapter quizzing, interactive chapter summaries, key term flashcards, marine biology video clips, and web links to chapter-related material.

Critical thinking questions challenge students to think more deeply about the chapter material and also help stimulate class discussion.

For Further Reading lists "General Interest" articles in publications such as *Scientific American, Discover,* and *National Geographic,* which are appropriate for students with limited backgrounds in science and "In Depth" readings for students who want to study particular topics in detail.

The World Ocean



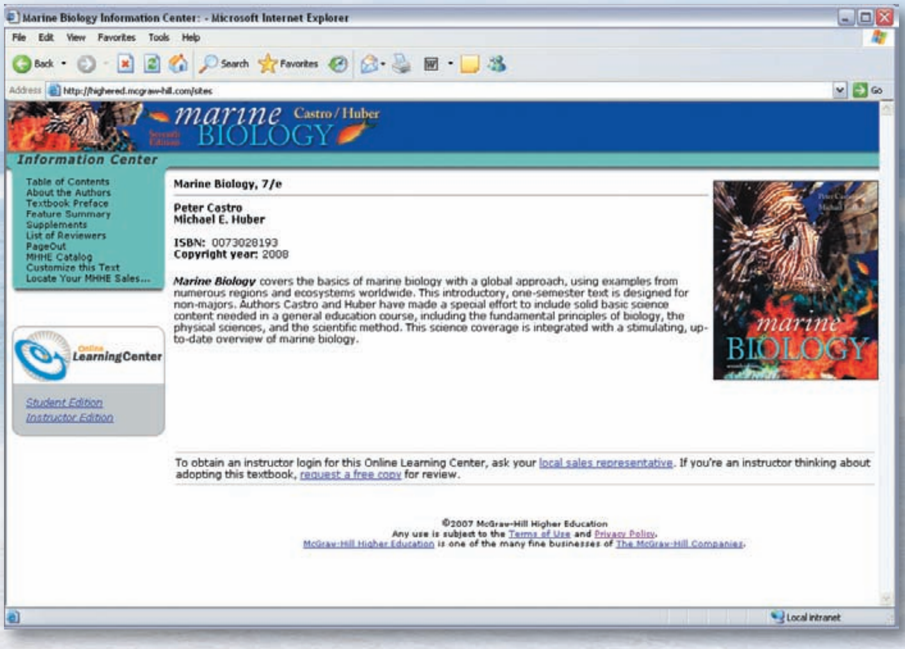
A foldout map at the end of text provides quick reference to the World Ocean and the major coastal marine ecosystems of North America.

Stay Afloat with the Marine Biology Online Learning Center!

www.mhhe.com/castrohuber7e

The ***Marine Biology*** **Online Learning Center** offers a wealth of learning and teaching aids for instructors and students

Instructors will appreciate a password-protected **Instructor's Manual,** containing **laboratory exercises,** and access to McGraw-Hill's new Presentation Center, including all of the illustrations, photographs, and tables from the text.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Marine Biology, 7/e

Peter Castro
Michael E. Huber

ISBN: 0073028193
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Marine Biology covers the basics of marine biology with a global approach, using examples from numerous regions and ecosystems worldwide. This introductory, one-semester text is designed for non-majors. Authors Castro and Huber have made a special effort to include solid basic science content needed in a general education course, including the fundamental principles of biology, the physical sciences, and the scientific method. This science coverage is integrated with a stimulating, up-to-date overview of marine biology.

To obtain an instructor login for this Online Learning Center, ask your local sales representative. If you're an instructor thinking about adopting this textbook, request a free copy for review.

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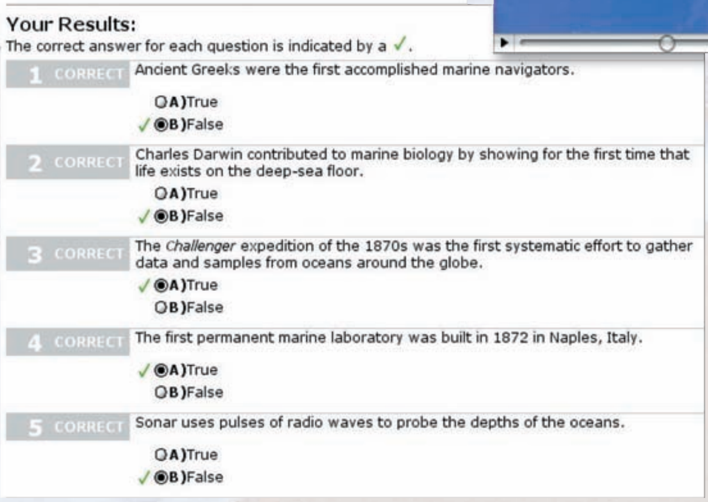
Students will benefit from **interactive quizzing, key term flashcards,** and **web links.** Also included are **underwater video clips,** featuring footage of marine animals, their behaviors, and ecosystems.

PREVIOUS • NEXT
cytoskeleton
CLICK TO SEE DEFINITION

A complex framework inside cells made of protein fibers.



Your Results:
The correct answer for each question is indicated by a ✓.

1 CORRECT Ancient Greeks were the first accomplished marine navigators.
○ A) True
✓ ● B) False

2 CORRECT Charles Darwin contributed to marine biology by showing for the first time that life exists on the deep-sea floor.
○ A) True
✓ ● B) False

3 CORRECT The *Challenger* expedition of the 1870s was the first systematic effort to gather data and samples from oceans around the globe.
✓ ● A) True
○ B) False

4 CORRECT The first permanent marine laboratory was built in 1872 in Naples, Italy.
✓ ● A) True
○ B) False

5 CORRECT Sonar uses pulses of radio waves to probe the depths of the oceans.
○ A) True
✓ ● B) False

Ancillaries

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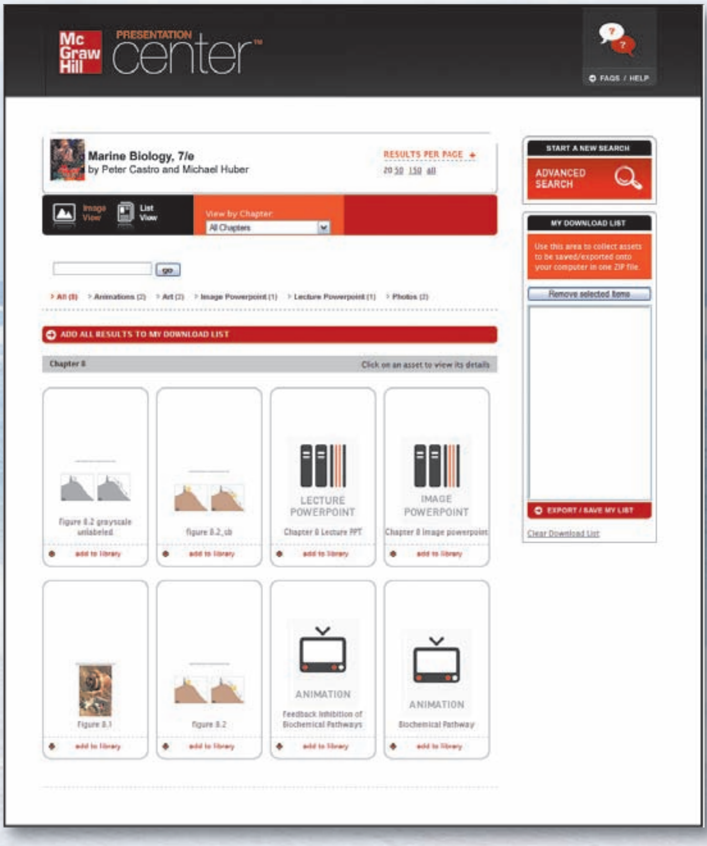
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Instructor's Manual

Prepared by Peter Castro, this helpful ancillary provides student learning outcomes for each chapter, chapter outlines and summaries, a listing of audiovisuals and software, and answers to the Critical Thinking questions within the text. Instructors will also find suggestions on presenting concepts to students and organizing materials for class presentation. The instructor's manual can be accessed via the password-protected portion of the ***Marine Biology* Online Learning Center.**

Test Bank

A computerized test bank utilizing testing software to quickly create customized exams is available with this text. The user-friendly software allows instructors to search for questions by topic or format, edit existing questions or add new ones, and scramble questions to create multiple versions of the same test. Word files of the test bank questions are provided for those instructors who prefer to work outside the test-generator software.

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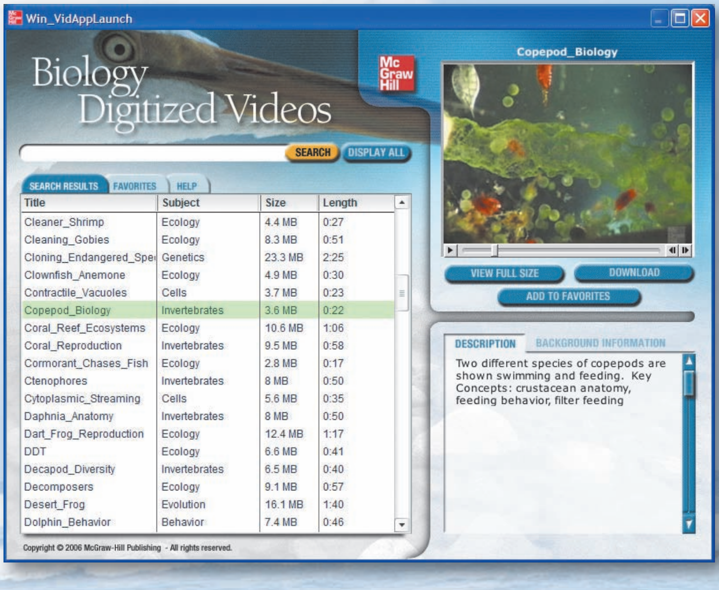

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Cloning_Endangered_Spe	Genetics	23.3 MB	2:25
Clownfish_Anemone	Ecology	4.9 MB	0:30
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Copepod_Biology	Invertebrates	3.6 MB	0:22
Coral_Reef_Ecosystems	Ecology	10.6 MB	1:06
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Cormorant_Chases_Fish	Ecology	2.8 MB	0:17
Ctenophores	Invertebrates	8 MB	0:50
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Dolphin_Behavior	Behavior	7.4 MB	0:46

Two different species of copepods are shown swimming and feeding. Key Concepts: crustacean anatomy, feeding behavior, filter feeding

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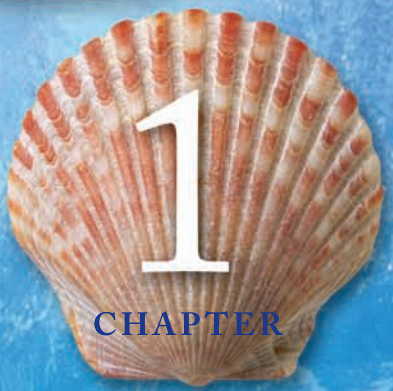
Laboratory Exercises

Ideal for a one-quarter or one-semester course, this collection of eight laboratories and field investigations in marine biology has been specially designed for use in conjunction with the seventh edition of ***Marine Biology.*** Each of the exercises includes review questions that integrate information learned in the laboratory or field with material covered in the text. The exercises can be accessed via the password-protected portion of the ***Marine Biology*** **Online Learning Center.**

Part One

Principles of Marine Science



CHAPTER 1

The Science of Marine Biology

A biologist weighs an Adélie penguin (*Pygoscelis adeliae*), one of many species losing habitat due to global climate change.

Marine biology is the scientific study of the organisms that live in the sea. The ocean is a vast realm, home to countless strange and wonderful creatures. It is often the beauty, mystery, and variety of life in the sea that attract students to a course in marine biology. Even professional marine biologists feel a sense of adventure and wonder in their studies.

There are also many practical reasons to study marine biology. Life on earth probably originated in the sea, so the study of marine organisms teaches us much about all life on earth, not just marine life. In the late nineteenth century, for example, the Russian scientist Ilya Metchnikof discovered cells of the animal immune system by studying sea anemones and the larvae of sea stars. His discovery underpins a great deal of modern medical research.

Marine life also represents a vast source of human wealth. It provides food, medicines, and raw materials; offers recreation to millions; and supports tourism all over the world. Marine organisms can also cause problems. For example, some organisms harm humans directly by causing disease or attacking people. Others harm us indirectly by injuring or killing other marine organisms that we value for food or other purposes. Some marine organisms erode piers, walls, and other structures we build in the ocean, foul ship bottoms, and clog pipes.

At a much more fundamental level, marine life helps determine the very nature of our planet. Marine organisms produce around half of the oxygen we breathe and help regulate the earth's climate. Our shorelines are shaped and protected by marine life, at least in part, and some marine organisms even help create new land. In economic terms, it has been estimated that the ocean's living systems are worth more than $20 *trillion* a year.

To make both full and wise use of the sea's living resources, to solve the problems marine organisms create, and to predict the effects of human activities on the life of the sea, we must learn all we can about marine life. In addition, marine organisms provide clues to the earth's past, the history of life, and even our own bodies that we must learn to understand. This is the challenge, the adventure, of marine biology.

THE SCIENCE OF MARINE BIOLOGY

Marine biology is not really a separate science but, rather, the more general science of biology applied to the sea. Nearly all the disciplines of biology are represented in marine biology. There are marine biologists who study the basic chemistry of living things, for example. Others are interested in whole organisms: the way they behave, where they live and why, and so on. Other marine biologists adopt a global perspective and look at the way entire oceans function as systems. Marine biology is thus both part of a broader science and itself made up of many different disciplines, approaches, and viewpoints.

Marine biology is closely related to oceanography, the scientific study of the oceans. Like marine biology, oceanography has many branches. Geological oceanographers, or marine geologists, study the sea floor. Chemical oceanographers study ocean chemistry, and physical oceanographers study waves, tides, currents, and other physical aspects of the sea. Marine biology is most closely related to biological oceanography, so closely, in fact, that the two are difficult to separate. Sometimes they are distinguished on the basis that marine biologists tend to study organisms living relatively close to shore, whereas biological oceanographers focus on life in the open ocean, far from land. Another common distinction is that marine biologists tend to study marine life from the perspective of the organisms (for example, studying how organisms produce organic matter), while biological oceanographers tend to take the perspective of the ocean (for example, studying how energy or organic matter cycles through the system). In practice there are so many exceptions to these distinctions that many marine scientists consider marine biology and biological oceanography to be the same.

A marine biologist's interests may also overlap broadly with those of biologists who study terrestrial organisms. Many of the basic ways in which living things make use of energy, for example, are similar whether an organism lives on land or in the sea. Nevertheless, marine biology does have a flavor all its own, partly because of its history.

The History of Marine Biology

People probably started learning about marine life from the first time they saw the ocean. After all, the sea is full of good things to eat. Archaeologists have found piles of shells, the remains of ancient "clambakes," dating back to the Stone Age. Ancient harpoons and simple fishhooks of bone or shell have also been found. While they gathered food, people learned through experience which things were good to eat and which were bad-tasting or harmful. The tomb of an Egyptian pharaoh, for example, bears a warning against eating poisonous pufferfishes. Ancient people used marine organisms for more than food. Snail shells were used for necklaces at least 75,000 years ago, for example. In using marine resources, coastal peoples in virtually every culture developed a store of practical knowledge about marine life and the oceans.

FIGURE 1.1 Micronesians like these Satawal Islanders from Yap Atoll in the Federated States of Micronesia navigated the Pacific for millennia in canoes much like this one.

Knowledge of the ocean and its organisms expanded as people gained skills in seamanship and navigation. Ancient Pacific Islanders had detailed knowledge of marine life, which their descendants still retain (Fig. 1.1). They were consummate mariners, using clues such as wind, wave, and current patterns to navigate over vast distances. The Phoenicians were the first accomplished Western navigators. By 2000 B.C. they were sailing around the Mediterranean Sea, Red Sea, eastern Atlantic Ocean, Black Sea, and Indian Ocean.

The ancient Greeks had considerable knowledge of nearshore organisms in the Mediterranean region (Fig. 1.2). The Greek philosopher Aristotle, who lived in the fourth century B.C., is considered by many to be the first marine biologist. He described many forms of marine life and recognized, among other things, that gills are the breathing apparatus of fish.

During the centuries known as the Dark Ages, scientific inquiry, including the study of marine life, came to a grinding halt in most of Europe. Much of the knowledge of the ancient Greeks was lost or distorted. Not all exploration of the ocean stopped, however. During the ninth and tenth centuries the Vikings continued to explore the northern Atlantic. In A.D. 995 a Viking party led by Leif Eriksson

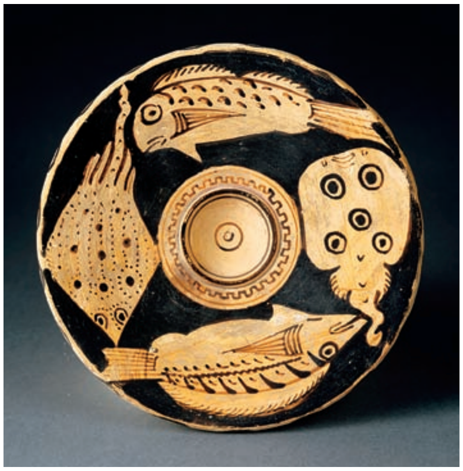


FIGURE 1.2
This Greek plate from around 330 B.C. reflects a considerable knowledge of marine life. The fish at the right is an electric ray (*Torpedo*), which the ancient Greeks used to deliver the first electrical stimulation therapy.

discovered Vinland, what we now call North America. Arab traders were also active during the Middle Ages, voyaging to eastern Africa, southeast Asia, and India. In the Far East and the Pacific, people also continued to explore and learn about the sea.

During the Renaissance, spurred in part by the rediscovery of ancient knowledge preserved by the Arabs, Europeans again began to investigate the world around them, and several undertook voyages of exploration. Christopher Columbus rediscovered the "New World" in 1492—word of the Vikings' find had never reached the rest of Europe. In 1519 Ferdinand Magellan embarked on the first expedition to sail around the globe. Many other epic voyages contributed to our knowledge of the oceans. Fairly accurate maps, especially of places outside Europe, began to appear for the first time.

Before long, explorers became curious about the ocean they sailed and the things that lived in it. An English sea captain, James Cook, was one of the first to make scientific observations along the way and to include a full-time naturalist among his crew. In a series of three great voyages, beginning in 1768, he explored all the oceans. He was the first European to see the Antarctic ice fields and to land in Hawai'i, New Zealand, Tahiti, and a host of other Pacific islands. Cook was the first to use a chronometer, an accurate timepiece that enabled him to accurately determine his longitude and therefore prepare reliable charts. From the Arctic to the Antarctic, from Alaska to Australia, Cook extended and reshaped the European conception of the world. He brought back specimens of plants and animals and tales of strange new lands. Though Cook was generally respectful and appreciative of indigenous cultures, he was killed in 1779 in a fight with native Hawaiians at Kealakekua Bay, Hawai'i.

By the nineteenth century, it had become common for vessels to take a naturalist along to study the organisms encountered. Perhaps the most famous of these shipboard naturalists was Charles Darwin, another Englishman. Beginning in 1831, Darwin sailed around the world on HMS *Beagle* for five years, horribly seasick most of the time. The *Beagle*'s primary mission was to map coastlines, but Darwin made detailed observations of all aspects of the natural world. This set off a train of thought that led him, years later, to propose the theory of evolution by natural selection (see "Natural Selection and Adaptation," p. 78). Though best known for the theory of evolution, Darwin made many other contributions to marine biology. He explained, for example, the formation of the distinctive rings of coral reef called atolls (see "How Atolls Form," p. 316). He used nets to capture the tiny, drifting organisms known as plankton, which marine biologists continue to do today (Fig. 1.3). Darwin's many interests also included barnacles. Specialists still refer to his treatise on them.

In the United States the most important early exploratory voyage was probably the United States Exploring Expedition of 1838–1842, often called the "Wilkes Expedition" after its leader, Lt. Charles Wilkes of the U.S. Navy. The expedition included only eleven naturalists and artists, derisively called "clam diggers" by the rest of the crew, and some historians conclude that it was more about projecting American influence than scientific discovery. Wilkes was by all accounts a vain and cruel man who promoted himself to Captain as soon as he left port, and upon his return was court-martialed for flogging his crew to excess. Only two of the expedition's six ships made it home. Nevertheless, the Wilkes Expedition's achievements were impressive. The expedition charted 2,400 km (1,500 mi) of the coast of Antarctica, confirming it as a continent, as well as the coast of the Pacific Northwest of North America. It explored some 280 islands in the South Pacific, collecting information about peoples and cultures as well as flora and fauna. The 10,000 biological specimens included some 2,000 previously unknown species (Fig. 1.4). The expedition, the first international survey sponsored by the United States government, also laid a foundation for government funding of scientific research.

The *Challenger* Expedition By the middle of the nineteenth century a few lucky scientists were able to undertake voyages specifically to study the oceans, instead of having to tag along on ships doing other jobs. One was Edward Forbes, who in the 1840s and 1850s carried out extensive dredging of the sea floor, mostly around his native Britain but also in the Aegean Sea and other places. Forbes died prematurely in 1854, at the age of 39, but was the most influential marine biologist of his day. He discovered many previously unknown organisms and recognized that sea-floor life varies at different depths (see "Biodiversity in the Deep Sea," p. 375). Perhaps his most important contribution, however, was to inspire new interest in the life of the sea floor.

Forbes's contemporaries and successors, especially from Britain, Germany, Scandinavia, and France, carried on his studies of sea-floor life. Their ships were poorly equipped and the voyages short, but their studies produced many interesting results. They were so successful, in fact, that British scientists managed to convince their government to fund the first major oceanographic expedition, under the scientific leadership of

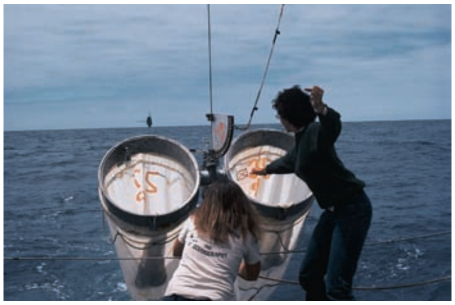


FIGURE 1.3
These marine scientists are hauling in a net known as a "bongo net" used to capture minute marine plankton. One is signaling instructions to the winch operator.

FIGURE 1.4 Peale's dolphin (*Lagenorhynchus australis*), named after the Wilkes Expedition naturalist who first described it, is one of 2,000 marine and terrestrial species discovered by the expedition.

Charles Wyville Thompson. The British navy supplied a light warship to be fitted out for the purpose. The ship was named HMS *Challenger.*

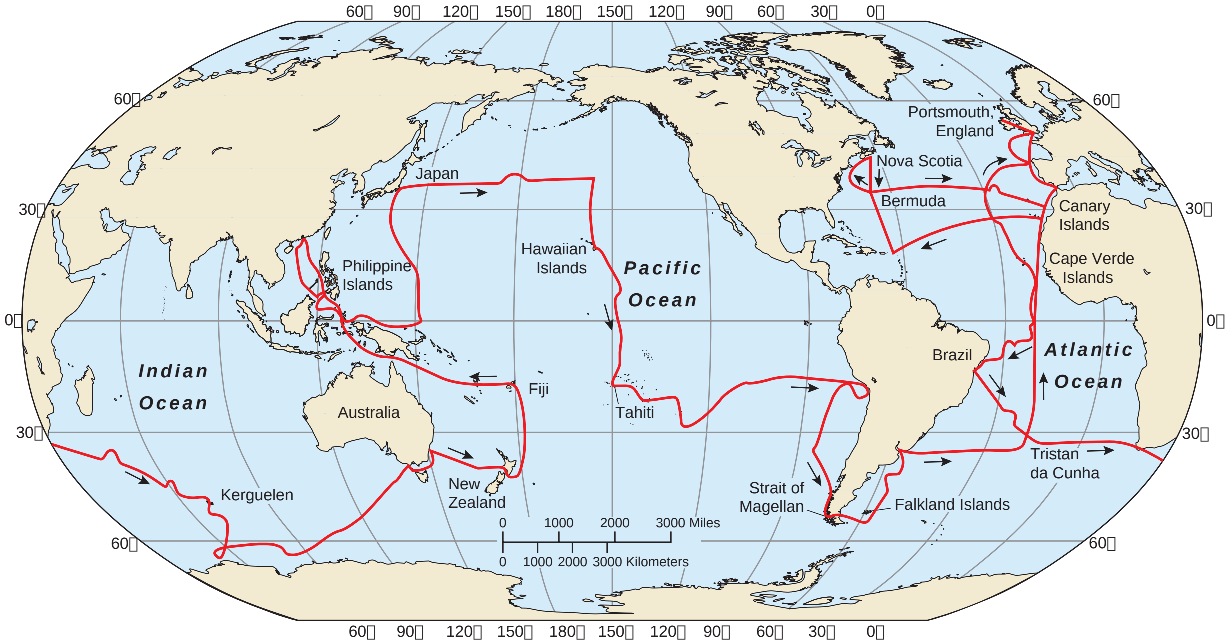
Challenger underwent extensive renovations in preparation for the voyage. Laboratories and quarters for the scientific crew were added, and gear for dredging and taking water samples in deep water was installed. Though primitive by modern standards, the scientific equipment on board was the best of its day. Finally, in December 1872, *Challenger* set off.

Over the next three and a half years, *Challenger* and her crew sailed around the world, gathering information and collecting samples (Fig. 1.5). The sheer volume of the data was enormous. After the *Challenger* expedition returned to port, it took 19 years to publish the results, which fill 50 thick volumes. *Challenger* brought back more information about the ocean than had been recorded in all previous human history.

It was not just the duration of the voyage or the amount of information collected that set the *Challenger* expedition apart from earlier efforts. The expedition set new standards for studying the ocean. Measurements were made systematically and carefully, and meticulous records were kept. The crew worked with great efficiency and dedication to the task. For the first time, scientists began to get a coherent picture of what the ocean was like. They also learned more about the enormous variety of marine life, for *Challenger* brought back thousands of previously unknown species. Thus, the *Challenger* expedition laid the foundations of modern marine science.

Other expeditions soon continued the work begun by *Challenger*, and major oceanographic cruises continue to this day. In many ways, though, the voyage of the *Challenger* remains one of the most important in the history of oceanography.

The Growth of Marine Labs Even before the *Challenger* set off, biologists were excited about the organisms brought back by ocean expeditions. Unfortunately, the vessels had quarters for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Canary Islands
Cape Verde Islands
Japan
Philippine Islands
Hawaiian Islands
Pacific Ocean
Indian Ocean
Brazil
Atlantic Ocean
Fiji
Tahiti
Australia
New Zealand
Kerguelen
Strait of Magellan
Falkland Islands
Tristan da Cunha
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FIGURE 1.5 The route of the *Challenger* expedition, which from 1872 to 1876 undertook the first systematic survey of the world ocean.

only a few scientists. Most biologists only got to see the dead, preserved specimens that the ships brought back to port. Such specimens revealed much about marine life around the world, but biologists wanted to know how the organisms actually lived: how they functioned and what they did. Living specimens were essential for this, but ships usually stayed in one place only for a short time, making long-term observations and experiments impossible.

Rather than study the ocean from ships, biologists began to work at the seashore. Among the first were two Frenchmen, Henri Milne Edwards and Victor Andouin, who around 1826 began making regular visits to the shore to study marine life. Other biologists soon followed suit. These excursions offered the opportunity to study live organisms, but there were no permanent facilities and only a limited amount of equipment could be taken along. This restricted the scope of the investigations. Eventually, biologists set up permanent laboratories where they could keep organisms alive and work over long periods. The first such laboratory was the Stazione Zoologica, founded in Naples, Italy, in 1872—the same year the *Challenger* embarked. The laboratory of the Marine Biological Society of the United Kingdom was founded at Plymouth, England, in 1879.

FIGURE 1.6 Scientists and crew at the Marine Biological Laboratory at Woods Hole, Massachusetts, *circa* 1888.

The first major American marine laboratory was the Marine Biological Laboratory at Woods Hole, Massachusetts. It is hard to pinpoint the exact date when this laboratory was established. The first marine laboratory at Woods Hole was started by the United States Fish Commission in 1871, but it did not flourish. Several other short-lived laboratories subsequently appeared in the area around Woods Hole. Harvard biologist Louis Agassiz, who also studied many of the specimens collected by the Wilkes Expedition, established a laboratory on nearby Cape Ann in 1873. In 1888 this laboratory moved to Woods Hole and officially opened its doors as the Marine Biological Laboratory (Fig. 1.6). It is still one of the world's most prestigious marine stations.

After these early beginnings, other marine laboratories were established. Among the earliest in the United States were the Hopkins Marine Station in Pacific Grove, California; Scripps Institution of Oceanography in La Jolla, California; and the Friday Harbor Marine Laboratory in Friday Harbor, Washington. In the ensuing years, more laboratories appeared all over the world, and new ones are being established even today.

The onset of World War II had a major effect on the development of marine biology. A new technology, **sonar,** or *so*und *na*vigation *r*anging, was developed in response to the growing importance of submarine warfare. Sonar is based on the detection of underwater echoes—a way of listening to the sea (Fig. 1.7). The ocean, long thought of as a silent realm, was suddenly found to be full of sound, much of it made by animals. During wartime, learning about these animals was no longer the casual pursuit of a few interested marine biologists but a matter of national security. As a result of this urgency, several marine laboratories, such as Scripps and the Woods Hole Oceanographic Institution (established in 1929), underwent rapid growth. When the war ended, these labs not only remained vital research centers but continued to grow.

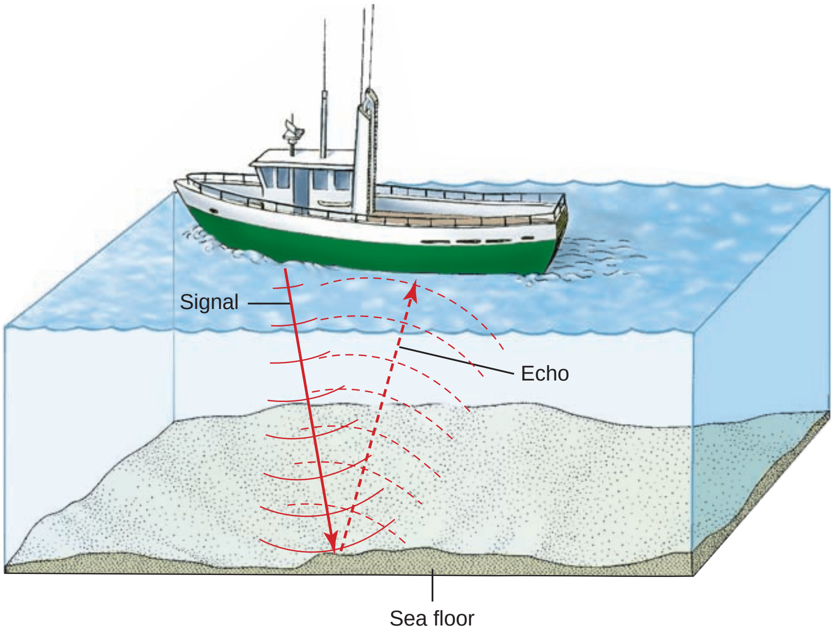
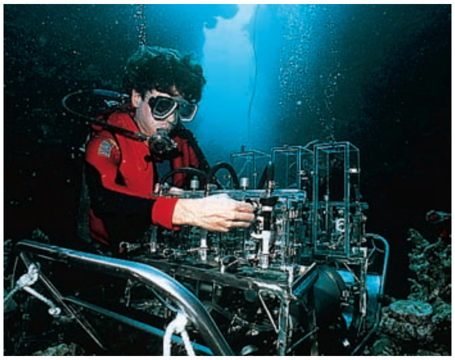


FIGURE 1.7 A ship uses sonar by "pinging," or emitting a loud pulse of sound, and timing how long it takes the echo to return from the sea floor. The water depth can be determined from the return time. This, the most common form of sonar, is called "active sonar" because the sounds used are actively generated by the equipment (see "Eyes (and Ears) in the Ocean," p. 12).

FIGURE 1.8 Scuba is an important tool in the work of many marine biologists. This scientist is using an apparatus called a respirometer to measure the production and consumption of oxygen by organisms on a coral reef.



The years immediately after World War II saw the refinement of the first practical **scuba,** or *s*elf-*c*ontained *u*nderwater *b*reathing *a*pparatus. The basic technology used in scuba was developed in occupied France by the engineer Émile Gagnan to allow automobiles to run on compressed natural gas. After the war, Gagnan and fellow Frenchman Jacques Cousteau modified the apparatus, using it to breathe compressed air under water. Cousteau went on to devote his life to scuba diving and the oceans.

Using scuba, marine biologists could, for the first time, descend below the surface to observe marine organisms in their natural environment (Fig. 1.8). They could now work comfortably in the ocean, collecting specimens and performing experiments, though they were still limited to relatively shallow water, generally less than 50 m (165 ft).

FIGURE 1.9 The R/V *Thomas G. Thompson*, operated by the University of Washington, was the first of a new generation of research vessels. These vessels offer increased work space and can travel to research sites more quickly and stay there longer than earlier research ships.

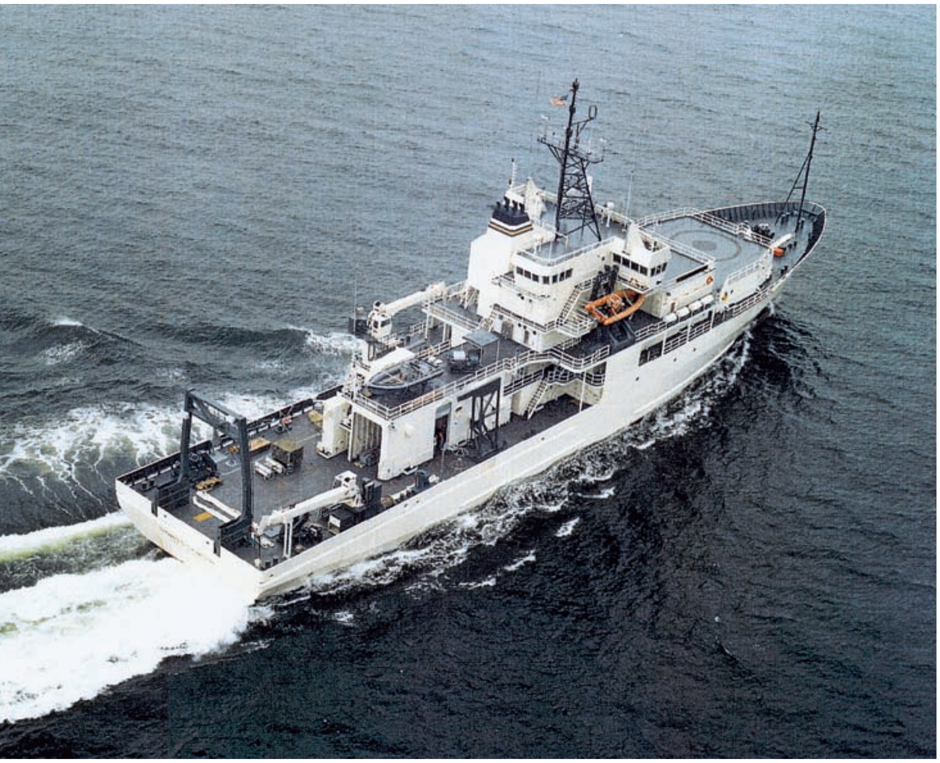
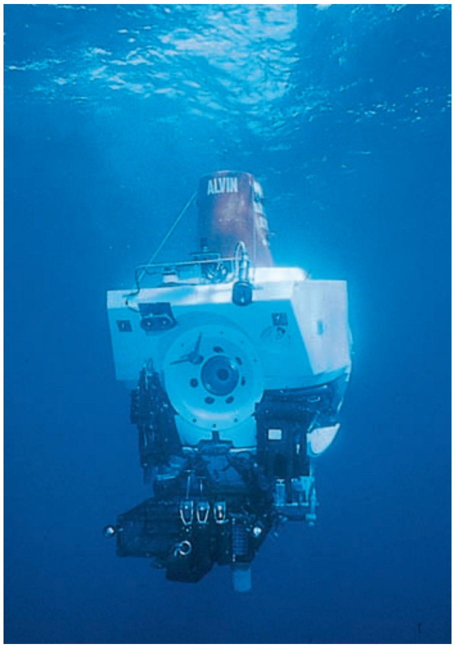


FIGURE 1.10 *Alvin,* a deep-sea submarine operated by the Woods Hole Oceanographic Institution, is one of the most famous vessels in the history of marine science.



Marine Biology Today

Oceanographic ships and shore-based laboratories are as important to marine biology now as they were in the past. Today many universities and other institutions operate research vessels (Fig. 1.9). Modern ships are equipped with the latest equipment for navigation, sampling, and studying the creatures that are collected. Many, like *Challenger,* were originally built for other uses, but a growing number of vessels are being custom-built for scientific research at sea.

In addition to ships as we normally think of them, some remarkable craft are used to study the marine world. High-tech submarines can descend to the deepest parts of the ocean, revealing a world that was once inaccessible (Fig. 1.10). A variety of odd-looking vessels ply the oceans, providing specialized facilities for marine scientists (Fig. 1.11). Marine biologists increasingly use underwater robots to take photos, make measurements, and collect samples in the ocean depths. Remotely operated vehicles (ROVs) are controlled from the surface, while autonomous underwater vehicles (AUVs; see Fig. 16.23) are preprogrammed to do their jobs independently of direct human control. Such vehicles may soon even be able to recognize and count different species of fish. Scientists have also developed automated instrument buoys that drift with the currents or are moored in place and collect oceanographic data over long periods, even permanently. Other instrument packages rest on the sea floor. Even marine animals can be used as "autonomous samplers." Penguins and elephant seals, for example, have been fitted with electronic sensors that record oceanographic data in the course of the animals' normal movements.

Marine laboratories, too, have come a long way since the early days. Today labs dot coastlines around the world and are used by an international community of scientists. Some are equipped with the most up-to-date facilities available. Others are simple field stations, providing a base for scientists to work in remote areas. There are even undersea habitats where scientists can live for weeks at a time, literally immersed in their work (Fig. 1.12).

Marine laboratories are important centers not only of research, but also of education. Many offer summer courses that allow students to learn about marine biology firsthand (Fig. 1.13). Most labs provide facilities for graduate students from various universities to pursue their studies, and some offer graduate degrees in marine biology on their own. Thus, in addition to furthering today's research, marine laboratories are busy training the professional marine biologists of tomorrow.

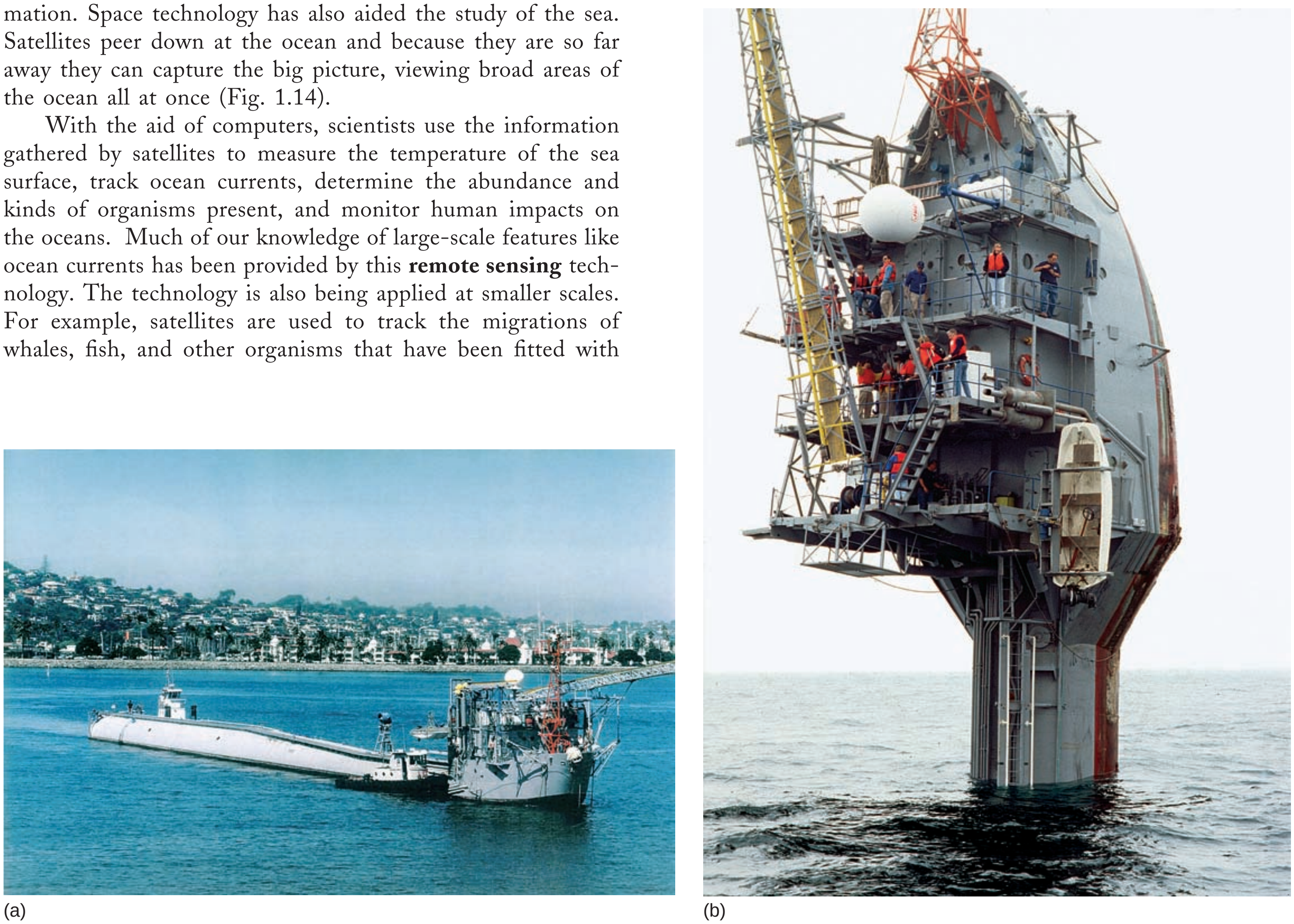
New technology offers exciting opportunities for the study of the oceans. Computers have had a huge impact because they allow scientists to rapidly analyze enormous amounts of information. Space technology has also aided the study of the sea. Satellites peer down at the ocean and because they are so far away they can capture the big picture, viewing broad areas of the ocean all at once (Fig. 1.14).

With the aid of computers, scientists use the information gathered by satellites to measure the temperature of the sea surface, track ocean currents, determine the abundance and kinds of organisms present, and monitor human impacts on the oceans. Much of our knowledge of large-scale features like ocean currents has been provided by this **remote sensing** technology. The technology is also being applied at smaller scales. For example, satellites are used to track the migrations of whales, fish, and other organisms that have been fitted with miniature transmitters. Electronic buoys released at oil spill sites drift along with the oil and are tracked by satellite to monitor the path of the spill. These are just a few of the many and ever-increasing applications of remote sensing.

Marine biologists today use every available tool in their study of the sea, even some decidedly low-tech ones (Fig. 1.15). Information about the ocean pours in at an ever-increasing pace. Much remains to be learned, however, and the oceans remain a realm of great mystery and excitement.

THE SCIENTIFIC METHOD

Marine biology is an adventure, to be sure, but it is also a science. Scientists, including marine biologists, share a certain way of looking at the world. Students of marine biology need to be familiar with this approach and how it affects our understanding of the natural world, including the ocean.


(a)

(b)

FIGURE 1.11 R/V *FLIP,* short for *fl*oating *i*nstrument *p*latform, operated by Scripps Institution of Oceanography, provides a stable platform for research at sea. (*a*) Most of the hull consists of a hollow tube that floats while the vessel is towed into position. When the hull is flooded and sinks, *FLIP* swings into a vertical position (*b*) in which it is largely unaffected by the rise and fall of waves.

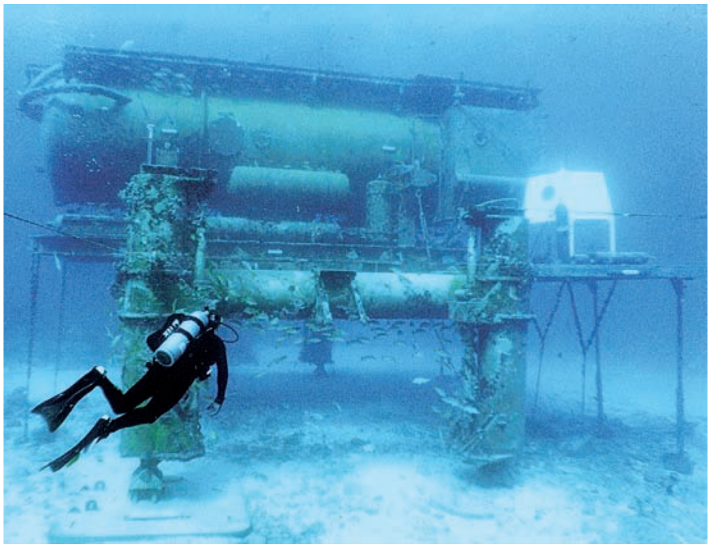
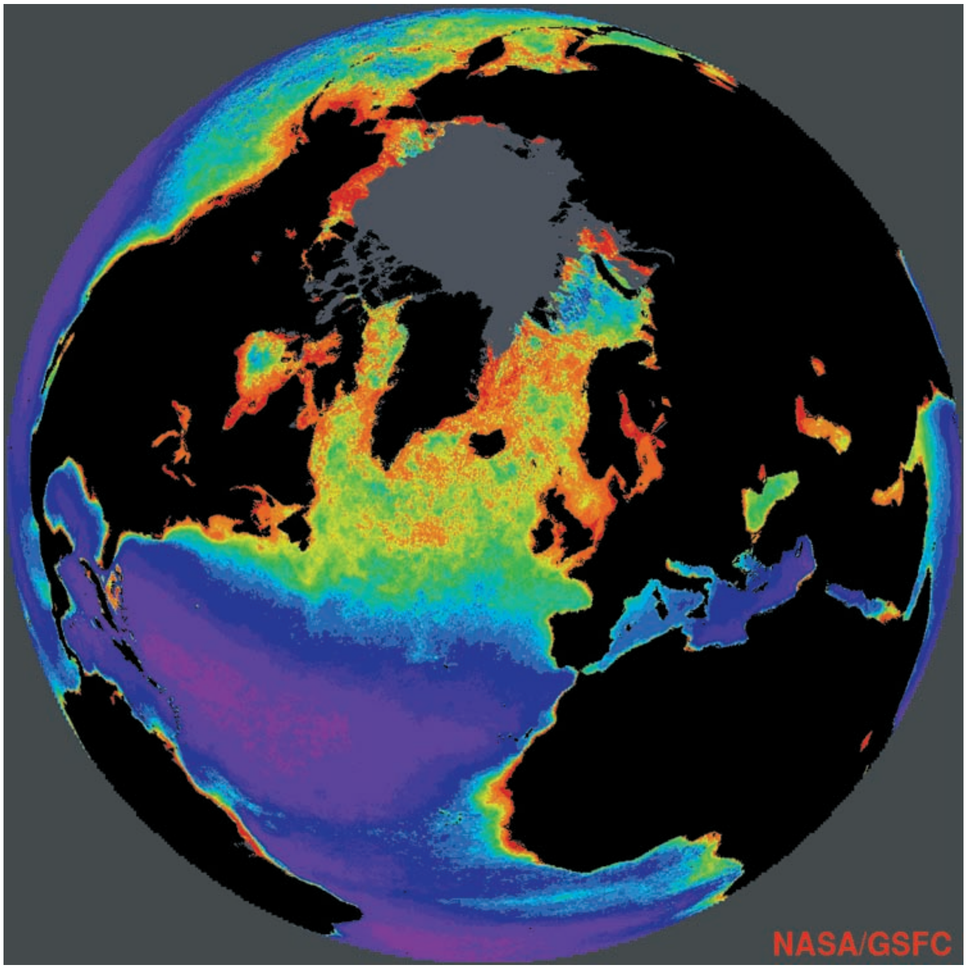


FIGURE 1.12 A diver swims outside *Aquarius,* the world's only underwater marine science laboratory. *Aquarius* is located in the Florida Keys Marine Sanctuary at a depth of about 20 m (60 ft). The living quarters are in the large cylinder at the upper left, which, fortunately for the crew, is larger than it appears here because it is further away than the diver.

FIGURE 1.13 A marine biology class at Duke University's marine laboratory in Beaufort, North Carolina.



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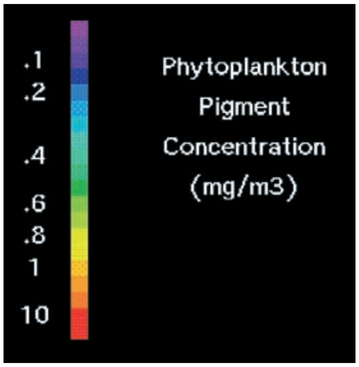


FIGURE 1.14 A satellite image showing the abundance of photosynthetic organisms in the ocean, as indicated by the amount of pigment in the water. This photo was taken by the Coastal Zone Color Scanner (CZCS), which was mounted on the *Nimbus-7* satellite. It is actually a composite of information gathered over nearly an eight-year period. Advances in computer and space technology made this image possible.

We live in an age of science. Advertisers constantly boast of new "scientific" improvements to their products. Newspapers regularly report new breakthroughs, and many television stations have special science reporters. Governments and private companies spend billions of dollars every year on scientific research and science education. Why has science come to occupy a position of such prestige in our society? The answer, quite simply, is that it works! Science has been among the most successful of human endeavors. Modern society could not exist without the knowledge and technology produced by science. The lives of almost everyone have been enriched by scientific advances in medicine, agriculture, communication, transportation, art, and countless other fields.

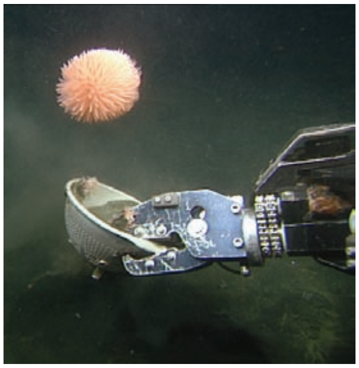


FIGURE 1.15 High-tech meets low-tech: The robotic arm of the ROV *Ventana* captures a pom-pom anemone *(Liponema brevicornis)* in an ordinary kitchen colander.

Much of the practical success of science results from the way it is done. Scientists do not see the world as a place where things happen for no reason. They assert instead that the universe can be explained by physical laws. Scientists don't go about discovering these laws haphazardly; they proceed according to time-tested procedures. The set of procedures by which scientists learn about the world is known as the **scientific method.**

Scientists sometimes disagree over the fine points of exactly what constitutes the scientific method. As a result, they may apply the method in slightly different ways. In spite of these minor differences, most scientists do agree on the basic principles of the scientific method, which should be seen as a flexible framework guiding the study of nature rather than a rigid set of rules.

Observation: The Currency of Science

The goal of science is to discover facts about the natural world and principles that explain these facts. At the heart of the scientific method is the conviction that we can learn about the world only through our senses or with tools that extend our senses. Microscopes, for example, extend our vision to help us see what is otherwise too small to be visible. Thus, scientific knowledge is fundamentally derived from the observation of nature. Scientific conclusions must be based on observations rather than on preexisting ideas of how the world is or should be.

One of the advantages of relying on observations is that they are accessible to others. A person's thoughts, feelings, and beliefs are internal. No one really knows what goes on in the mind of another. On the other hand, the world studied by scientists is external to any single person. Different people can look at the same object. Even though sensory perception may be imperfect and scientists, like anyone else, are not always impartial, the object is there for all to see. Thus, there is a way to check and verify any one person's observations.

Observation is critical to all phases of the scientific method. To begin with, it allows us to describe the natural world. The only way to learn what organisms live in a particular part of the ocean, how many of them there are, how fast and how large they grow, when and how they reproduce, what they eat, how they behave, and so on is to observe that part of the ocean and the organisms living there. Exploration and description are vitally important parts of marine biology, constantly revealing new information. Previously unknown species, for example, are found practically every time the deep-sea floor is sampled (see "Biodiversity in the Deep Sea," p. 375). New technologies, such as underwater cameras that reveal the behavior of whales (see "Eyes (and Ears) in the Ocean," p. 12) or genetic techniques that have uncovered vast numbers of previously unknown marine microbes (see "Tiny Cells, Big Surprises," p. 92), regularly improve our ability to observe the sea and make new discoveries. Each finding leads to new observations. The discovery of completely unknown and unexpected ecosystems at deep-sea hot springs, for example, led biologists to look for—and find—similar ecosystems in other parts of the ocean (see "Hot Springs, Cold Seeps, and Dead Bodies," p. 374).

As they observe more and more about the world, scientists inevitably seek to explain their observations—*why is that species of seaweed found only in a certain depth range?*—and to make predictions—*will the fishing be good next year?* The desire to explain and predict in turn guides yet more observation.

Two Ways of Thinking

To describe, explain, and make predictions about the natural world, scientists use two basic forms of thinking. In **induction** one uses separate observations to arrive at general principles. Reasoning from general principles to specific conclusions is called **deduction.** Once there were heated arguments over which way of thinking was acceptable, but scientists now generally agree that both induction and deduction are indispensable.

Induction When using induction, a scientist starts with a series of individual observations. Ideally, he or she has no goal or preconceptions about the outcome and is completely objective. The scientist then uses these observations to reach a general conclusion. For example, suppose a marine biologist examined a sailfish (Fig. 1.16), a shark (Fig. 1.17), and a tuna (Fig. 1.18) and found that they all had gills. Because sailfishes, sharks, and tunas are all fishes, he might draw the general conclusion *All fishes have gills.* This is an example of induction.

In the process of induction, general conclusions are made on the basis of specific observations.

EYE ON SCIENCE

Ocean Observing Systems

What is happening in one place in the ever-changing ocean is usually linked to other places, so understanding the ocean requires systematic, long-term observations of many places at once. In the first attempts to make such observations, multiple research ships simultaneously collected data from different locations, but ships are very expensive and have to return to port—and scientists can get seasick. Improving technologies such as satellites, moored and drifting instrument buoys, sea-floor instruments, ROVs and AUVs, and underwater cameras have steadily improved our ability to make unmanned observations (see "Marine Biology Today," p. 6). Ocean scientists are now integrating these technologies, and new ones being developed, into a permanent Global Ocean Observation System (GOOS) that will provide a continuous window on the entire world ocean.

Some parts of the system are already in place. The Argo system consists of automated floats scattered throughout the ocean that measure water temperature and salinity. Each float descends to a depth of 2,000 m (6,600 ft), drifts with the current for about 10 days, and surfaces to transmit data via satellite before sinking to start a new cycle. The first floats were launched in 2000 and some 3,000 floats now dot the oceans. Argo is an important addition to systems of moored, solar-powered buoys that transmit similar data from many parts of the ocean.

Solar power and data transmission by satellite work fine at the surface, but not under water. There aren't any electrical outlets or phone jacks on the sea floor, so scientists are wiring the ocean to bring power and communications to an amazing array of instrumentation. There will be instruments to measure ocean currents and chemistry, detect the slightest sea-floor tremors, and track biological activity. Many of these technologies are ready to go. Others, such as genomic sensors that will not only measure the abundance of plankton but also identify them from their DNA, are still on the drawing board. In addition to permanent instrumentation there will be docking stations where free-ranging AUVs can charge batteries and download photographs and data, junction boxes where additional instruments can be plugged in as new experiments are designed and new technology becomes available, hydrophones to gather data from buoys, and even instruments attached to animals, all augmented by ship- and satellite-based systems. Scientists are even working on AUVs that can catch plankton and use it to generate their own power.

Cables for the first sea-floor observatory in the United States, the Long-term Ecosystem Observatory (LEO-15), were installed off the coast of New Jersey in 1996. As LEO-15 was steadily integrated with underwater gliders, shore-based radar, ship measurements, and moored surface instruments, it evolved into the New Jersey Shelf Observing System. This system has greatly improved understanding of the area's oceanography, and is delivering practical benefits to people, for example by helping forecast the track of Tropical Storm Ernesto, which struck the area in 2006. There are plans to connect the system to other cabled observatories to cover much of the East Coast of the United States. The first cables for a new-generation system in the Pacific, the Victoria Experimental Network Under the Sea (VENUS) were laid in 2006 in Saanich Inlet, on the coast of British Columbia, Canada. Installation of another cabled observatory, the Monterey Accelerated Research System (MARS), commenced in 2007. VENUS and MARS are the testing grounds for a much larger system, the North East Pacific Time-integrated Undersea Networked Experiments (NEPTUNE) Observatory. NEPTUNE will extend from British Columbia to Oregon and wire up the entire tectonic Plate of Juan de Fuca.

It will take decades for these and similar systems being developed in Europe, Japan, and other places to be fully operational, but they are already revealing much about the ocean. Eventually they will allow students and teachers everywhere to see first-hand what's going on in the sea; help forecast earthquakes, tsunamis, and storms; and allow scientists to monitor fish populations. Ocean observatories will one day save both lives and money and help humanity make wiser use of the oceans—and indeed the entire ocean planet.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

The scientist must be careful in using induction. The step from isolated observations to general conclusion critically depends on the number and quality of the observations and on recognizing their limitations. If the biologist stopped after examining the sailfish, which happens to have a bill, he might use induction to make the false conclusion *All fishes have bills.* Even after examining all three fishes, he might have concluded *All marine animals have gills* instead of just *All fishes have gills.* This is where deduction comes into play.

Deduction In deduction, scientists start with a general statement about nature and predict what the specific consequences would be if that statement is true. The general statement might be based on hunch or intuition, but it is usually based on observations. Suppose our marine biologist used induction to make the general statement *All marine animals have gills.* He might then

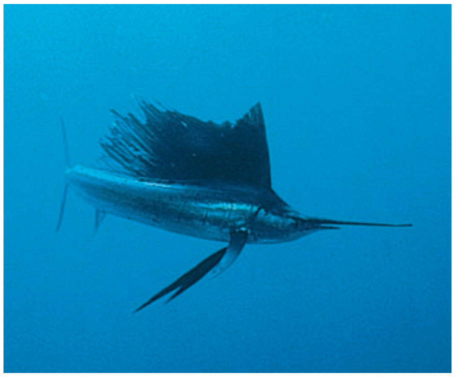
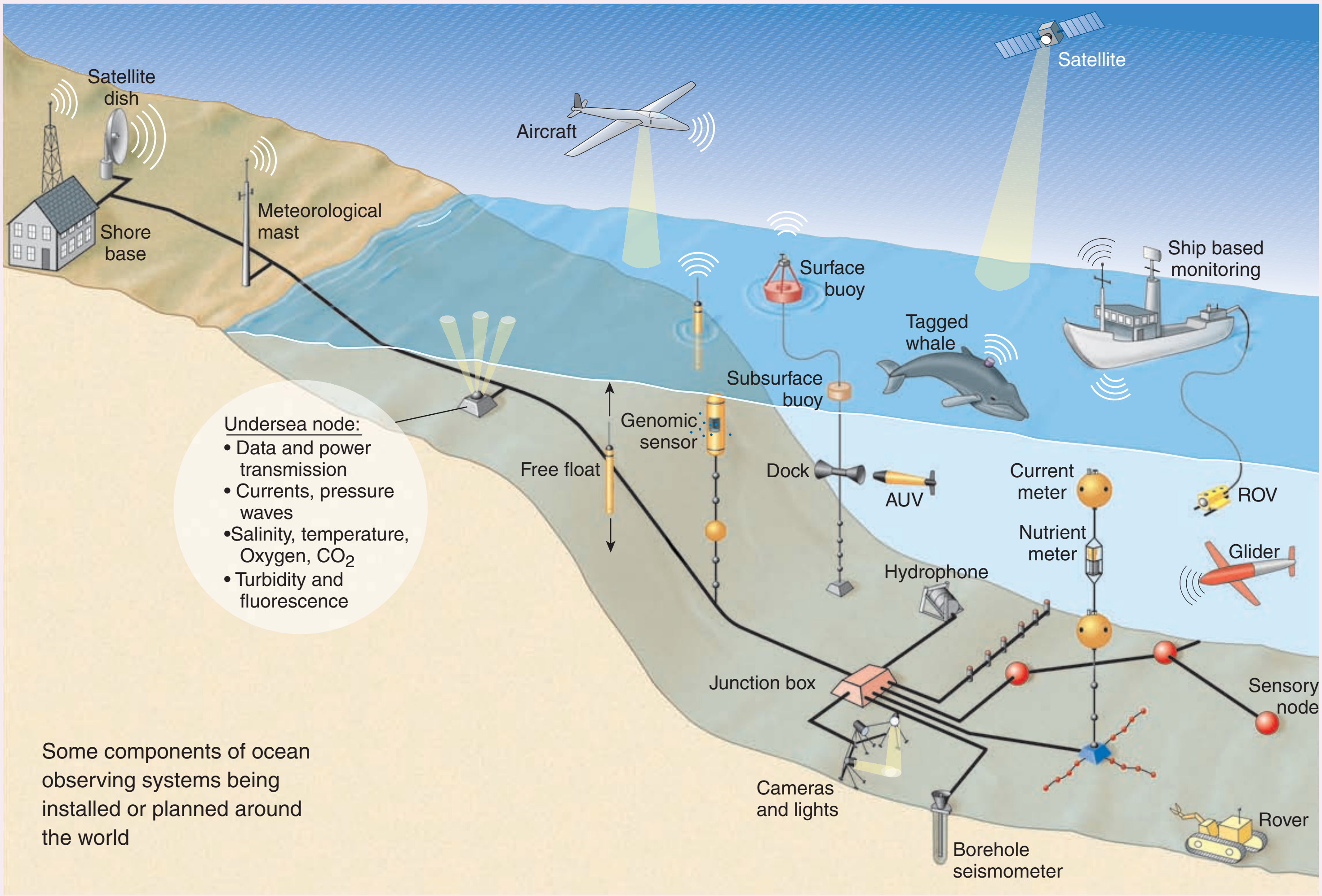


FIGURE 1.16
The Indo-Pacific sailfish (*Istiophorus platypterus*). The long projection on the snout is called the bill.


Satellite dish
Shore base
Meteorological mast
Aircraft
Satellite
Surface buoy
Ship based monitoring
Tagged whale
Subsurface buoy
Undersea node:
• Data and power transmission
• Currents, pressure waves
•Salinity, temperature, Oxygen, CO_2
• Turbidity and fluorescence
Genomic sensor
Free float
Dock
AUV
Current meter
ROV
Nutrient meter
Glider
Hydrophone
Junction box
Sensory node
Cameras and lights
Borehole seismometer
Rover

Some components of ocean observing systems being installed or planned around the world

reason that if all marine animals have gills and whales are marine animals, then whales must have gills. The biologist has used a general statement about all marine animals to make a statement about a particular kind of marine animal.

> In the process of deduction, specific predictions are made by applying general principles.

Testing Ideas

Scientists are never content to simply make statements about the world and let it go at that. Instead, they are obsessed with testing the statements to see whether they are, in fact, true. Both induction and deduction lead the scientist to make statements that *might* be true. A statement that might be true is called a **hypothesis.** A crucial feature of the scientific method is that all hypotheses are tested, usually again and again. This insistence on testing is one of the great strengths of the scientific method. Incorrect hypotheses are usually quickly weeded out and discarded.

> The term "fish" is used for a single individual or for more than one individual of the same species.
> The term "fishes" is used to refer to more than one species of fish.

Eyes (and Ears) in the Ocean

Marine biologists are often frustrated by how hard it is to actually *see* what is going on in the ocean. They can collect samples with nets and dredges, make measurements with automated instruments, and do experiments in the laboratory, and in these ways have learned a great deal about marine life. We humans are visual creatures, though, and no amount of sampling, measurement, or experimentation can completely substitute for actually watching organisms in their natural habitats.

One solution is to go into the ocean for a look. Scuba and research submersibles have tremendously aided the study of the ocean, allowing us not only to see the organisms we study, but also to conduct experiments in the natural environment. These methods have their limitations, though. Scuba divers can penetrate only the shallowest parts of the ocean, and then only for short periods of a few hours at most. Scuba diving is also physically demanding. Submarines are extremely expensive and accommodate only a very few very cramped scientists at a time. Compared to fishes, whales, seals, and other fast-moving animals, both scuba divers and submarines are slow, cumbersome, and highly intrusive.

Another approach is to use still or video cameras that operate automatically or can be controlled from the surface. Such cameras are unlikely to be in the right place at the right time just by chance, so bait is often used to attract the animals of interest to the camera (see Fig. 16.26). Such systems have captured new and unusual deep-sea animals on film and provided useful information about their lifestyles.

Observing the complex behavior of large marine animals like seals, sea lions, and whales has always been a problem. They move too fast, too deep, and too far for a human diver, much less a stationary camera, to possibly record their behavior. Even if people could keep up with them we would be a disruptive presence, and the animals would be unlikely to behave normally. So, why not let the animals themselves take the pictures? "Crittercam" is a compact underwater video camera that can be attached to animals including sea turtles, sharks, whales, seals, and sea lions. Our knowledge of these animals' behavior once came almost entirely from watching them on land and at the surface. Crittercam lets us observe them under water, where they spend most of their time. This has given us new insight into their lives. Recently, for example, Crittercam recorded the first underwater views of humpback whales using curtains of bubbles to herd schools of herring into a tight ball before rocketing into the school to feed. Similarly, miniature digital cameras attached to Adélie *(Pygoscelis adeliae)* and chinstrap *(P. antarctica)* penguins have revealed that the penguins often dive in social groups, and "turtlecams" have been used to study endangered sea turtles in Mexico.

Not all efforts to "see" in the ocean rely on vision as we normally think of it. Light does not penetrate very far in seawater (see "Transparency," p. 47), which means not only that most of the ocean is too dark to see, but also that even with artificial light visibility is quite limited. Sound, by contrast, travels long distances under water, which is the basis of sonar. Modern sonar and computerized data processing produce detailed three-dimensional images of the sea floor (see Figs. 2.20 and 2.21). Instead of generating their own sound, "passive" sonar systems take advantage of existing background noise from waves, ships, animals, and other sources. Sound bouncing off an object—a whale, for example—can be picked up by underwater microphones and, with the aid of computers, processed into moving images. Such systems can work in the dark, potentially over relatively long distances, and reduce noise disturbance to the animals. Ships may soon use passive sonar to avoid collisions with unseen whales.

Wearing Crittercam doesn't seem to bother this female northern elephant seal (*Mirounga angustirostris*) or her neighbors. The ability to record social behavior with minimal human interference is one of Crittercam's advantages.

New technology is also being used to spy on tiny plankton. These organisms are among the most important on earth, but until recently had to be studied mainly by catching them in nets. This usually damages or kills them. At the very least it removes them from their environment and completely disrupts their natural behavior. Imagine how limited our understanding of birds would be if our knowledge was based entirely on catching them in nets towed behind airplanes!

Some systems for visualizing plankton rely solely on video. Four cameras are required to accurately track these organisms in their three-dimensional world, which lacks fixed reference points. Other systems use a kind of sonar, or a combination of sonar and video. The sonar is used to determine the organisms' size and position, and when they are in range a digital camera takes a snapshot using a red flash, which most of the organisms can't see. Still other systems use lasers to produce three-dimensional holograms of the tiny organisms that can be stored in a computer and examined in the laboratory. All these systems are giving us revealing new glimpses of life in the ocean.

Constructing the Hypothesis Scientific hypotheses must be stated in a way that allows them to be tested. What this means is that it must be possible, at least potentially, to *prove* that the hypothesis is false if it really is false. Sometimes this is simple. For example, the hypothesis that whales have gills is easy to test. All the biologist has to do is examine a whale to see whether it has gills. By doing so, he would find that whales have lungs, not gills (Fig. 1.19). He would have proven the hypothesis *Whales have gills* false. He would also disprove the more general hypothesis *All marine animals have gills.* The steps our marine biologist used to construct and test these hypotheses are illustrated in Figure 1.20. Actually, this line of reasoning is not entirely imaginary. Aristotle, one of the first marine biologists, used similar logic in the fourth century B.C. He observed not only that whales breathe with lungs and not gills, but that unlike most fishes they give birth to live young instead of laying eggs. Unfortunately, Aristotle's recognition that whales and other marine mammals are not fishes was lost to Western science for more than two millennia.

Hypotheses are often much more complicated than whether or not an animal has gills. Marine organisms are affected by weather and current patterns, the abundance of food and predators, natural cycles of reproduction and death, human activities, and a host of other factors. Marine scientists increasingly express their understanding of how such factors interact by constructing models, in the form of mathematical equations and computer programs, that predict what should happen in a given set of circumstances. However complex, such models constitute hypotheses that can be tested by comparing their predictions with what actually occurs in nature.

People sometimes make the mistake of proposing hypotheses that cannot be fairly tested. Someone who believes in mermaids might say, *Somewhere in the ocean there are mermaids.* The problem with this hypothesis is that it could never be *proved* to be false. An army of marine biologists could spend their entire careers looking for a mermaid without success, but the true believer could always say, *The mermaids are there; you just didn't find them.* No matter how hard they looked, the biologists could never prove that there are no mermaids. Therefore, the statement *There are mermaids in the ocean* is not a valid scientific hypothesis because it is not **testable.**

A scientific hypothesis is a statement about the world that might be true and is testable. A testable hypothesis is one that at least potentially can be proved false.

The Nature of Scientific Proof It must be possible to disprove a hypothesis, at least in principle, before the hypothesis can be considered scientific. But how can a hypothesis be proved to be true? This question has always troubled scientists, and the answer may trouble you too. In general, no scientific hypothesis can be absolutely proved true. For example, consider the hypothesis that all fishes have gills. It is easy to see that this hypothesis can be proved false by finding a fish without gills. But even though every fish so far examined has gills, this does not prove that *all* fishes have gills. Somewhere out there may lurk a fish without them. Just as it cannot be proved that there are no mermaids, it can never be proved that all fish have gills.

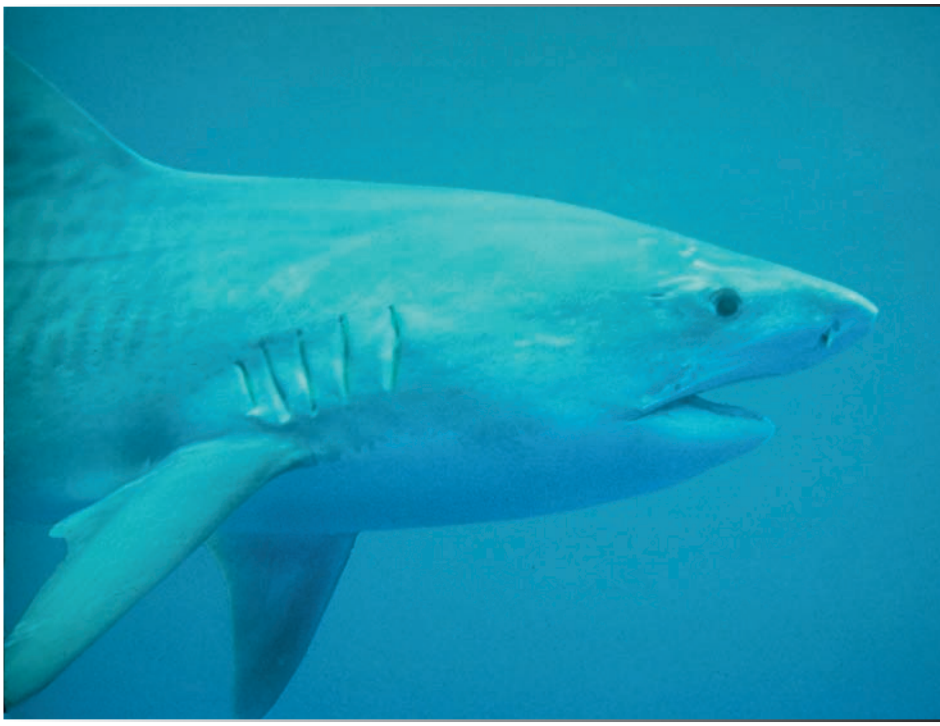


FIGURE 1.17 A tiger shark (*Galeocerdo cuvier*). The five vertical gill slits can be seen just in front of the pectoral fins.

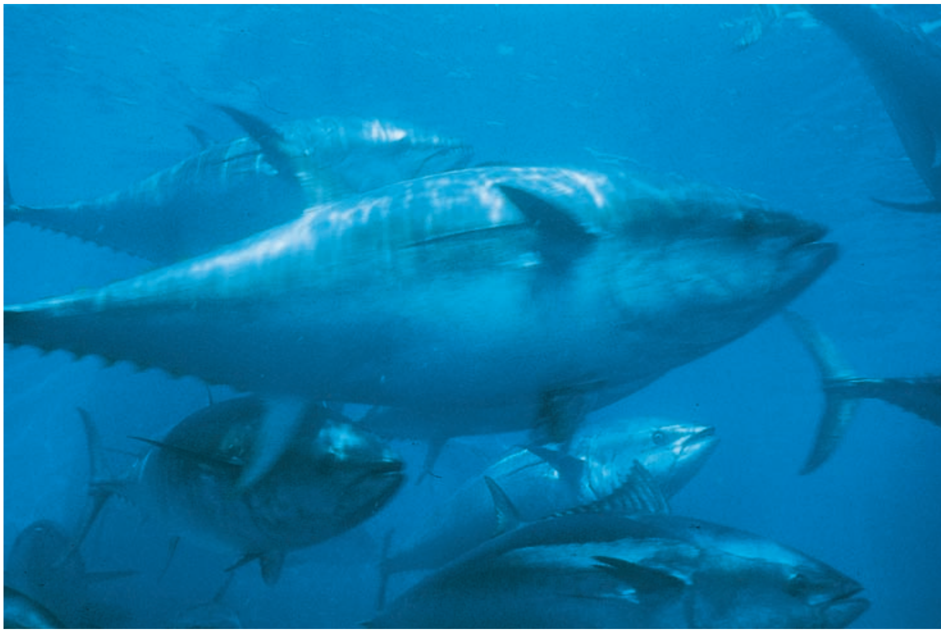


FIGURE 1.18 The northern bluefin tuna (*Thunnus thynnus*). These fish grow to nearly 700 kg (1,500 lb).

In science, then, there are no absolute truths. Knowing this, scientists could throw up their hands and look for another line of work. Fortunately, most scientists have learned to accept and deal with the lack of absolute certainty that is

John Steinbeck and Ed Ricketts

Most people know the American writer John Steinbeck as the author of such beloved works as *The Grapes of Wrath, Of Mice and Men,* and *East of Eden.* Less well known are Steinbeck's contributions to marine biology, which resulted largely from his close friendship with a man named Ed Ricketts.

Steinbeck and Ricketts first met in 1930—by Steinbeck's account, in a dentist's office in Pacific Grove, California. Steinbeck had a longstanding interest in marine biology and had wanted to meet Ricketts for some time. Ricketts owned the Pacific Biological Laboratory, located near the Hopkins Marine Station and the present site of the Monterey Bay Aquarium. Ricketts collected specimens of marine life along the Pacific coast and sold them to universities and museums. He was immensely popular in the area and knew more about marine biology than anyone around.

The two men became close friends almost immediately. Before long Steinbeck, then struggling as a writer, was spending a lot of time hanging around his friend's laboratory, going on collecting trips, and assisting in day-to-day operations. Steinbeck got so involved in this work that he could even get excited about a microscope:

> *My dream for some time in the future is a research scope with an oil immersion lens, but that costs about 600 dollars and I'm not getting it right now. . . . Oh boy! Oh boy! Sometime I'll have one.*[1]

John Steinbeck would eventually credit Ricketts with shaping his views of humanity and the world, and characters in at least six of Steinbeck's novels were based on Ricketts. The most famous is Doc, the main character of *Cannery Row,* who runs the "Western Biological Laboratory":

Ed Ricketts.

---

[1] From *Steinbeck: A Life in Letters* by Elaine A. Steinbeck and Robert Wallsten, editors, copyright 1952 by John Steinbeck, © 1969 by The Estate of John Steinbeck, © 1975 by Elaine A. Steinbeck and Robert Wallsten. Used by permission of Viking Penguin, a division of Penguin Putnam Inc.

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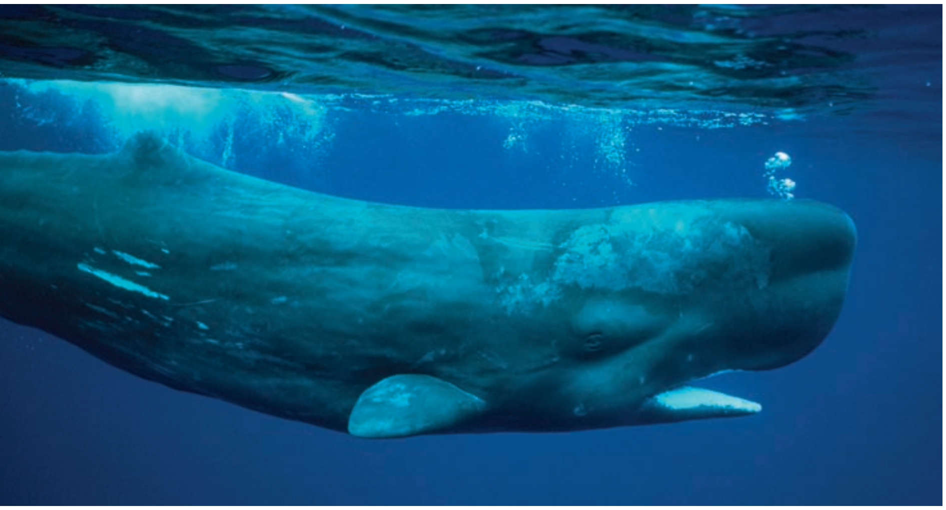
inherent in science by making the best of the available evidence. Any scientific hypothesis is examined and tested, poked and prodded, to see if it agrees with actual observations of the world. When a hypothesis withstands all these tests, it is conditionally accepted as "true" in the sense that it is consistent with the available information. Scientists speak of *accepting* hypotheses, not *proving* them. They accept the hypothesis that all fish have gills because every attempt to reject it has failed. At least for the time being, the hypothesis fits the observations. The good scientist, however, never quite forgets that any hypothesis, even a favorite one, could suddenly be thrown out the window by new information. No hypothesis is exempt from testing, and none is immune to being discarded if it conflicts with the evidence. The bottom line in science is observation of the world, *not* preconceived human ideas or beliefs.

FIGURE 1.19 A sperm whale (*Physeter catodon*) exhales bubbles of air from its lungs through the blowhole on top of its head.



No hypothesis can be scientifically *proved* to be true. Instead, hypotheses are *accepted* for as long as they are supported by the available evidence.

Testing the Hypothesis Because hypotheses generally can't be proved to be true, scientists, somewhat

> *It sells the lovely animals of the sea, the sponges, tunicates, anemones, the stars and buttlestars [sic], the sunstars, the bivalves, barnacles, the worms and shells, the fabulous and multiform little brothers, the living moving flowers of the sea, nudibranchs and tectibranchs, the spiked and nobbed and needly urchins, the crabs and demi-crabs, the little dragons, the snapping shrimps, the ghost shrimps so transparent that they hardly throw a shadow. . . . You can order anything living from Western Biological and sooner or later you will get it.*[2]

The friendship was beneficial to marine biology as well as to literature. Their expedition to Mexico produced *The Sea of Cortez,* a scientific report that is also part literature and part travelogue. The book lists the more than 600 species collected by the pair, including some 60 that were new to science. The trip was not all work, however: The authors report taking "2,160 individuals of two species of beer."

Ed Ricketts's most enduring contribution to marine biology was the 1939 publication *Between Pacific Tides.* Written with Jack Calvin, a friend of Ricketts and Steinbeck, *Between Pacific Tides* is a comprehensive guide to the seashore life of the Pacific coast of North America. Revised and updated, it is still used by amateurs and professionals alike.

Though Ricketts was an able biologist and was largely responsible for the content of *Between Pacific Tides,* he had difficulty getting his observations and ideas down on paper. Steinbeck almost certainly helped him write the book and get it published. When Ricketts felt that the publisher, Stanford University Press, was dragging its feet, Steinbeck fired off this sarcastic letter:

> *Gentlemen:*
>
> *May we withdraw certain selected parts of* Between Pacific Tides *which with the passing years badly need revision. Science advances but Stanford Press does not.*
>
> *There is the problem also of the impending New Ice Age.*
>
> *Sometime in the near future we should like to place our order for one (1) copy of the forthcoming (1948, no doubt) publication, The Internal Combustion Engine, Will it Work?*[3]
>
> *Sincerely,*
> *John Steinbeck*
> *Ed Ricketts*
>
> *P.S. Good Luck with A Brief Anatomy of the Turtle.*

Ed Ricketts was killed in a train accident in 1948. Steinbeck, saddened at the death of his friend, wrote, "There died the greatest man I have ever known and the best teacher."

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[2] From *Cannery Row*, by John Steinbeck. Copyright 1945 by John Steinbeck. Renewed © 1973 by Elaine Steinbeck, John Steinbeck IV, and Thom Steinbeck. Used by permission of Viking Penguin, a division of Penguin Putnam Inc.

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surprisingly, spend much of their time trying to disprove, not prove, hypotheses. More confidence can be placed in a hypothesis that has stood up to hard testing than in an untested one. Thus, the role of the scientist is to be a skeptic.

Often scientists are trying to decide among two or more **alternative hypotheses.** After looking at the sailfish, shark, and tuna, our imaginary marine biologist advanced two possible hypotheses: that all fish have gills and that all marine animals have gills. Both hypotheses were consistent with his observations to that point. After examining a whale, he rejected the second hypothesis and, in doing so, strengthened the first one. He arrived at the best hypothesis by a process of elimination.

Real marine biologists rarely have it as easy as our imaginary one, who was able to construct and then test his hypotheses about gills with just a few simple observations. Hypothesis testing usually requires carefully planned, painstaking observations. Occasionally a new observation or set of observations leads to the complete rejection of an accepted hypothesis, which has been termed a "scientific revolution." Such discoveries make headlines, but most of the time the scientific process is a gradual one in which hypotheses are continually refined and modified, and new alternatives proposed, as more information becomes available.

Hypotheses can often be tested by making the right kind of observations of the natural world, at the right time and place. Improved observing systems (see "Ocean Observing Systems," p. 10) will undoubtedly teach us a great deal about the ocean.

Sometimes, however, the conditions needed to test a hypothesis do not occur naturally and scientists must manipulate nature, that is, perform an **experiment,** to make the necessary observations.

In experiments, scientists create artificial situations to test hypotheses because they cannot make the necessary observations under natural conditions.

Suppose another marine biologist decides she wants to find out how water temperature affects the growth of mussels. She might be able to find two places, one warm and one cold, and measure how fast mussels grow at each place. The temperature at any given place changes all the time, however, and she would probably have difficulty finding two locations where one is always warmer than the other. Even if she does, the difference in temperature would not stay the same and there would probably be many other differences between the two places. The mussels might be different, for example. They might be eating

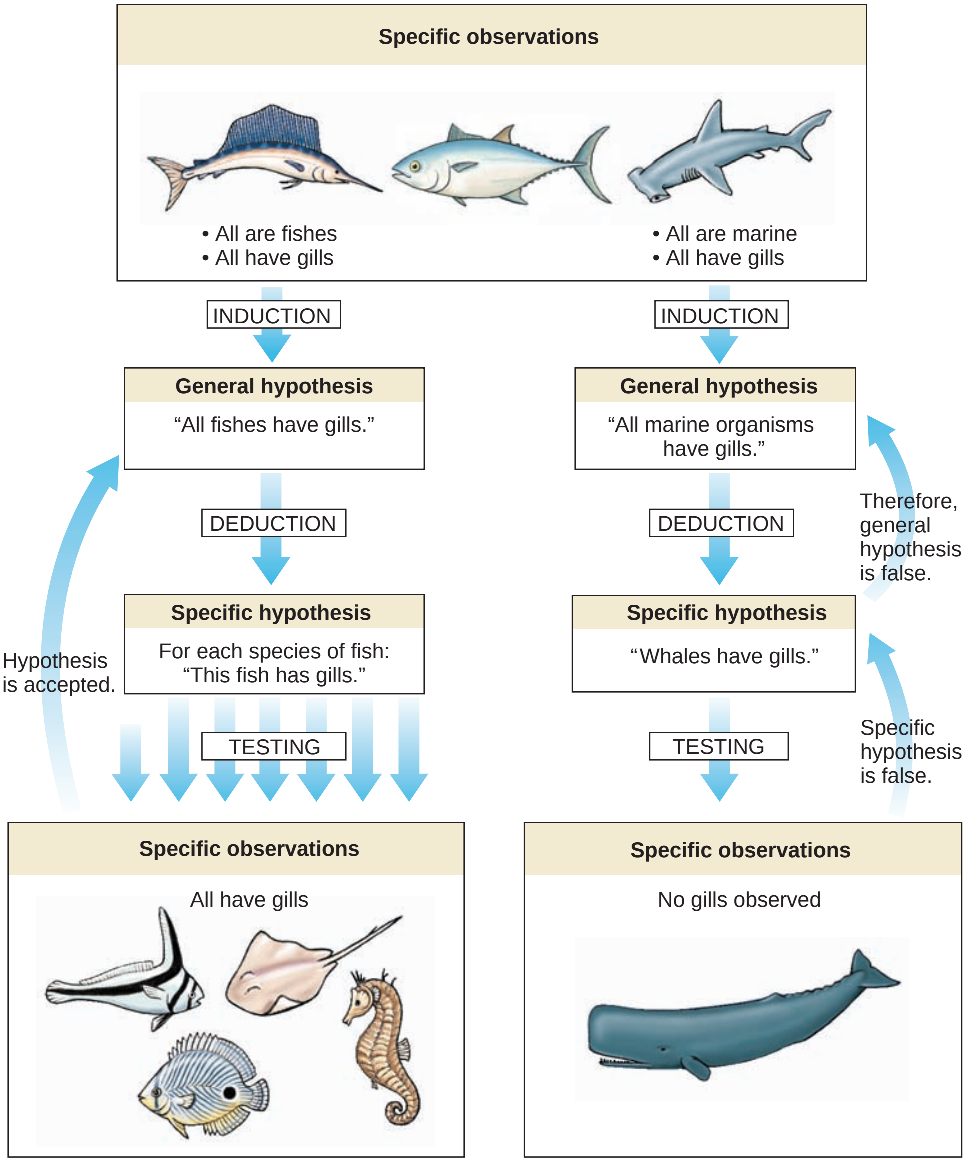

Specific observations
• All are fishes
• All have gills
• All are marine
• All have gills
INDUCTION
INDUCTION
General hypothesis
"All fishes have gills."
General hypothesis
"All marine organisms have gills."
DEDUCTION
DEDUCTION
Therefore, general hypothesis is false.
Specific hypothesis
For each species of fish: "This fish has gills."
Specific hypothesis
"Whales have gills."
Hypothesis is accepted.
TESTING
TESTING
Specific hypothesis is false.
Specific observations
All have gills
Specific observations
No gills observed

FIGURE 1.20 An example of the use of the scientific method. Two hypotheses were derived from the same observations. When tested by further observations, one hypothesis (left) is accepted and one (right) is rejected.

different foods or different amounts of food. There might be pollution or an outbreak of disease at one of the sites. In any natural situation, there would be countless factors other than temperature that could explain differences in mussel growth. Factors that might affect observations are called **variables.**

Faced with all these variables, the biologist decides to perform an experiment. She collects mussels from one place and divides them at random into two groups. Now she knows that the mussels in the two groups are pretty much the same. She places the two groups into tanks where she can control the water temperature and grows one group in warm water, the other in cold. She feeds all the mussels the same amounts of the same food at the same time, protects the mussels from pollution and disease, supplies both holding tanks with seawater from the same source, and keeps all the other living conditions exactly the same for both groups. Because all these variables are the same for both groups, the biologist knows that they cannot be responsible for any differences observed in mussel growth. The only difference between the two groups is temperature.

To prevent a variable from affecting an experiment, the scientist has two options. One is to artificially keep the variable from changing—for example, by giving all the mussels exactly the same food. The other is to make sure that any changes that do occur are identical for both groups. By supplying both tanks with seawater from the same source, for example, our biologist ensures that any changes that might occur in the quality of the water affect both groups of mussels equally. Variables that are prevented from affecting an experiment are said to be **controlled,** and the experiment is called a **controlled experiment** (Fig. 1.21). Since the biologist has controlled the effects of other variables while growing the mussels at different temperatures, she can be more confident that any observed difference in growth rate between the two groups is due to temperature.

Similarly, the biologist could study how food supply affects mussel growth by keeping the mussels at the same temperature but giving them different amounts of food. Experiments thus allow the effects of different variables to be separated. The way that variables interact can also be studied. The mussels could be maintained in different *combinations* of temperature and food supply, for example, to see whether the temperature at which they grow fastest depends on how much food they get.

The Scientific Theory Many people think of a theory as a rather shaky proposition, and most of us have heard people ridicule some idea or other because it was "only theoretical." The public usually reserves such scorn for controversial or unpopular theories. The theory of gravity, for instance, is rarely criticized for being "only a theory." In reality, a scientific theory is on much firmer ground than many people realize. A scientific **theory** is a hypothesis that has passed so many tests that it is generally accepted as true. In science, the status of theory is a lofty one indeed. Because it has been extensively tested, scientists place considerable confidence in it. They use it as a framework to order their thinking and move on to new discoveries.

It must be remembered, however, that a theory is still a hypothesis, albeit a well-tested one. As with other hypotheses, theories cannot be absolutely proved and are accepted as true only as long as they are supported by evidence. Good scientists

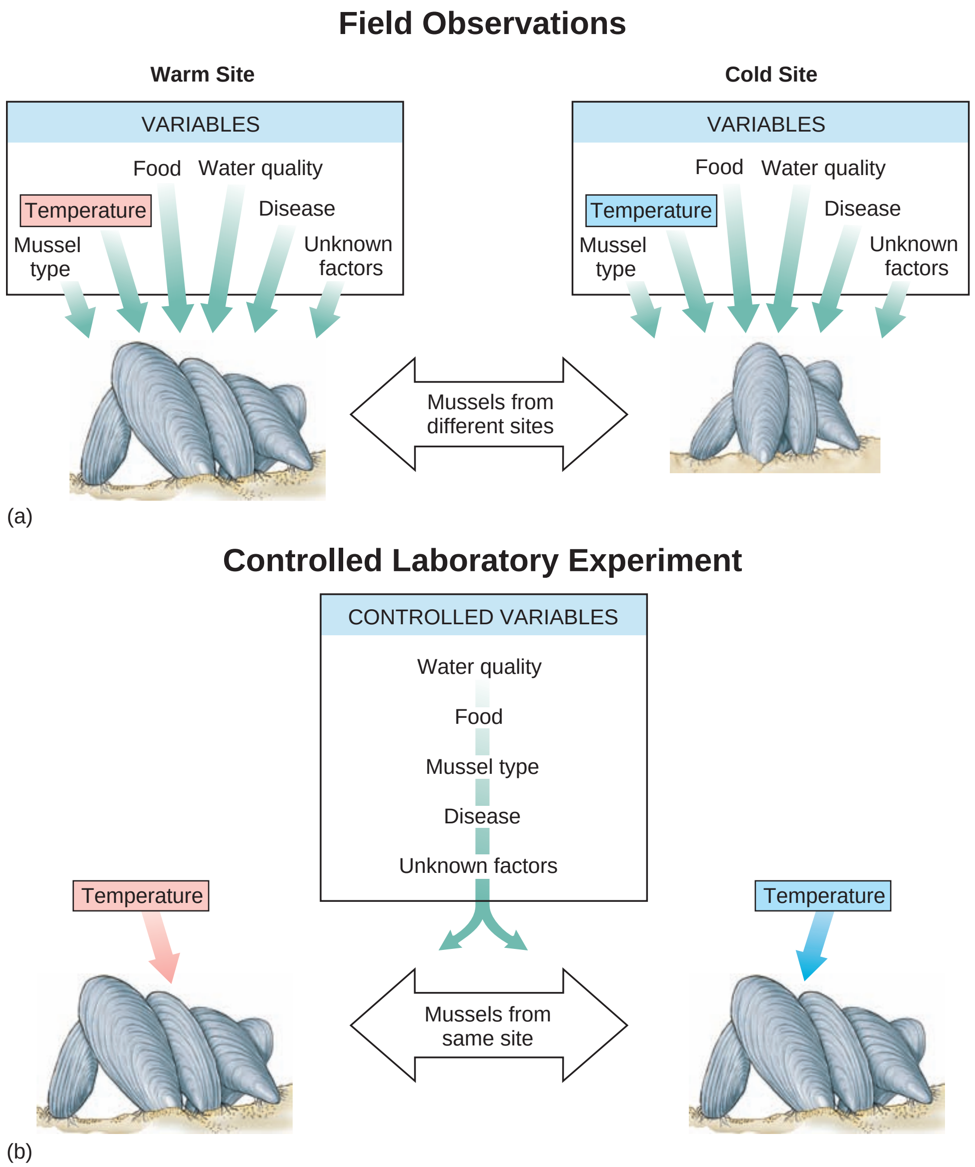

Field Observations
Warm Site
VARIABLES
Food
Water quality
Temperature
Disease
Mussel type
Unknown factors
Cold Site
VARIABLES
Food
Water quality
Temperature
Disease
Mussel type
Unknown factors
Mussels from different sites
(a)
Controlled Laboratory Experiment
CONTROLLED VARIABLES
Water quality
Food
Mussel type
Disease
Unknown factors
Temperature
Temperature
Mussels from same site
(b)

FIGURE 1.21 (*a*) Many different variables might produce differences between groups of mussels observed at two different locations. (*b*) Controlling the variables in an experiment allows the effects of a single factor—in this case, temperature—to be tested. This example describes a laboratory experiment, but experiments are often performed in the field (for example, see "Transplantation, Removal, and Caging Experiments," p. 252).

accept theories for the time being because the best available evidence supports them. They also recognize that any theory could be overturned by new evidence.

A scientific theory is a hypothesis that has been so extensively tested that it is generally regarded as true. Like any hypothesis, however, it is subject to rejection if enough evidence accumulates against it.

Limitations of the Scientific Method

No human enterprise, including science, is perfect. Just as it is important to understand how and why the scientific method works, it is important to understand the limitations of the scientific method. For one thing, remember that scientists are people too; they are prone to the same human shortcomings as anyone else. Scientists may be attached to favorite theories even when confronted with contradictory evidence—being wrong can be hard to accept. Like anyone else, they may let personal biases affect their thinking. No one can be completely objective all the time. Fortunately, factual errors are usually corrected because hypotheses are tested not just by one person but by many. The practical success of science is evidence that the self-checking nature of the scientific method does work most of the time.

Science also has some built-in limitations. Ironically, these limitations arise from the same features that give the scientific method its power: the insistence on direct observation and testable hypotheses. This means that science cannot make judgments about values, ethics, or morality. Science can reveal how the world is, but not how it should be. Science cannot decide what is beautiful. Science can't even tell humanity how to use the knowledge and technology it produces. These things all depend on values, feelings, and beliefs, which are beyond the scope of science.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Most of the major advances in marine biology have come in the last 200 years. What do you think are the reasons for this?
2. Recall that the statement "There are mermaids in the ocean is not a valid scientific hypothesis. Can the same be said of the statement There are *no* mermaids in the ocean?" Why?
3. Imagine you are a marine biologist and you notice that a certain type of crab tends to be larger in a local bay than in the waters outside the bay. What hypotheses might account for this difference? How would you go about testing these hypotheses?
4. Many species of whale have been hunted to the brink of extinction. Many people think that we do not have the right to kill whales and that all whaling should cease. On the other hand, in many cultures whales have been hunted for centuries and still have great cultural importance. People from such cultures argue that limited whaling should be allowed to continue. What is the role that science can play in deciding who is right? What questions cannot be answered by science?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

Chave, A., 2004. Seeding the seafloor with observatories. *Oceanus,* vol. 42, no. 2, pp. 28–31. Networks of high-tech instruments being established on the sea floor will allow us to continuously monitor ocean conditions and the internal dynamics of the earth.

Clarke, T., 2003. Oceanography: Robots in the deep. *Nature,* vol. 421, no. 6922, 30 January, pp. 468–470. Autonomous underwater vehicles—AUVs—are coming of age.

Linden, E., 2004. The Vikings: A memorable visit to America. *Smithsonian,* vol. 35, no. 9, December, pp. 92–99. The story of the Vikings' discovery of North America—and where they went when they left.

Mayr, E., 2000. Darwin's influence on modern thought. *Scientific American,* vol. 283, no. 1, July, pp. 78–83. Darwin's ideas and writings had a profound influence not only on science but also on society at large.

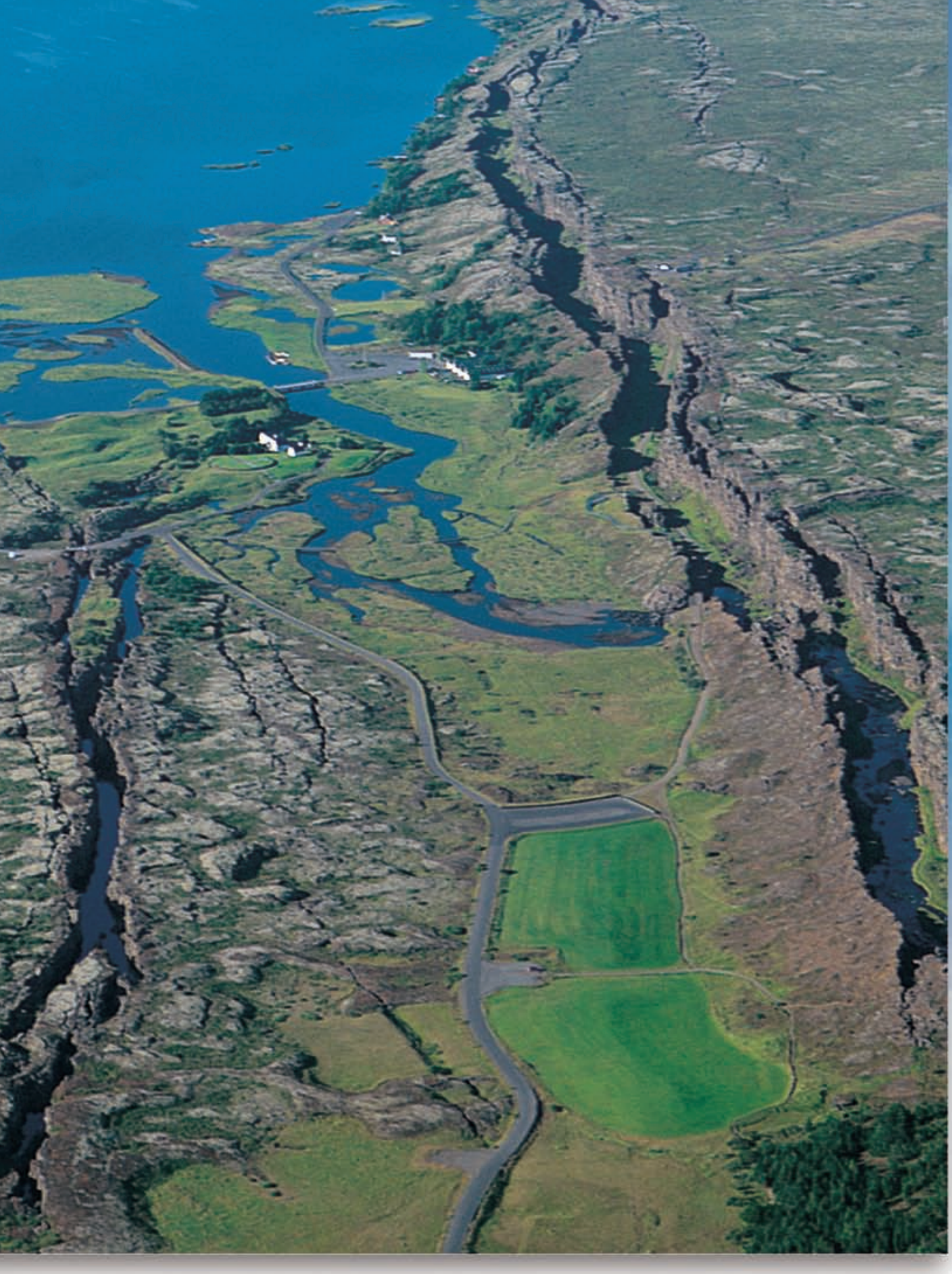
Ocean observatories. *Oceanus,* vol. 42, no. 1, 2000. High-tech instrument packages stay deep in the oceans for months, even years, at a time, sending back key information to scientists on the surface.

Stone, G. S., 2003. Deep science. *National Geographic,* vol. 204, no. 3, September, pp. 78–93. *Aquarius,* the world's only live-in underwater laboratory, lies on the sea floor in the Florida Keys.

Sulloway, F. J., 2006. The evolution of Charles Darwin. *Smithsonian,* vol. 36, no. 9, December, pp. 58–69. Darwin rigorously followed the scientific method, even when his conclusions challenged his deeply held religous beliefs.

Tindall, B., 2004. Tidal attraction. *Sierra,* vol. 89, no. 3, May/June, pp. 48–55, 64. A look at the same tide pools studied by Ed Ricketts and John Steinbeck—but many aren't what they once were.

Wheelwright, J., 2003. Sea searchers. *Smithsonian,* vol. 33, no. 10, January, pp. 56–62. Scientists launch an unprecedented effort to track the movements of marine animals using the latest electronics and satellite technology.



A portion of the mid-Atlantic ridge above the sea surface in Iceland.

2

CHAPTER

The Sea Floor

The oceans are not just places where the land happens to be covered by water. The sea floor is geologically distinct from the continents. It is locked in a perpetual cycle of birth and destruction that shapes the oceans and controls much of the geology and geological history of the continents. Geological processes beneath the waters of the sea affect not only the oceans, but dry land as well.

Most of the processes that mold ocean basins occur slowly, over hundreds of millions of years. On this timescale, where a human lifetime is but the blink of an eye, solid rocks flow like liquid, entire continents move across the face of the earth, and mountains grow from flat plains. To understand the sea floor, we must learn to adopt the unfamiliar perspective of geological time.

At first glance geology might not seem to have much to do with marine biology, but, day to day and over aeons, geological processes profoundly influence marine **habitats,** the natural environments where marine organisms live. Geological processes sculpt the shoreline; determine the water depth; control whether the bottom is muddy, sandy, or rocky; create new islands and undersea mountains for organisms to colonize; and determine the nature of marine habitats in countless other ways. Indeed, much of the history of life in the oceans has been determined by geological events.

THE WATER PLANET

Our planet is very much a water planet, unique in having large amounts of liquid water—the oceans—on its surface. The oceans not only cover 71% of the globe, but also regulate its climate and atmosphere.

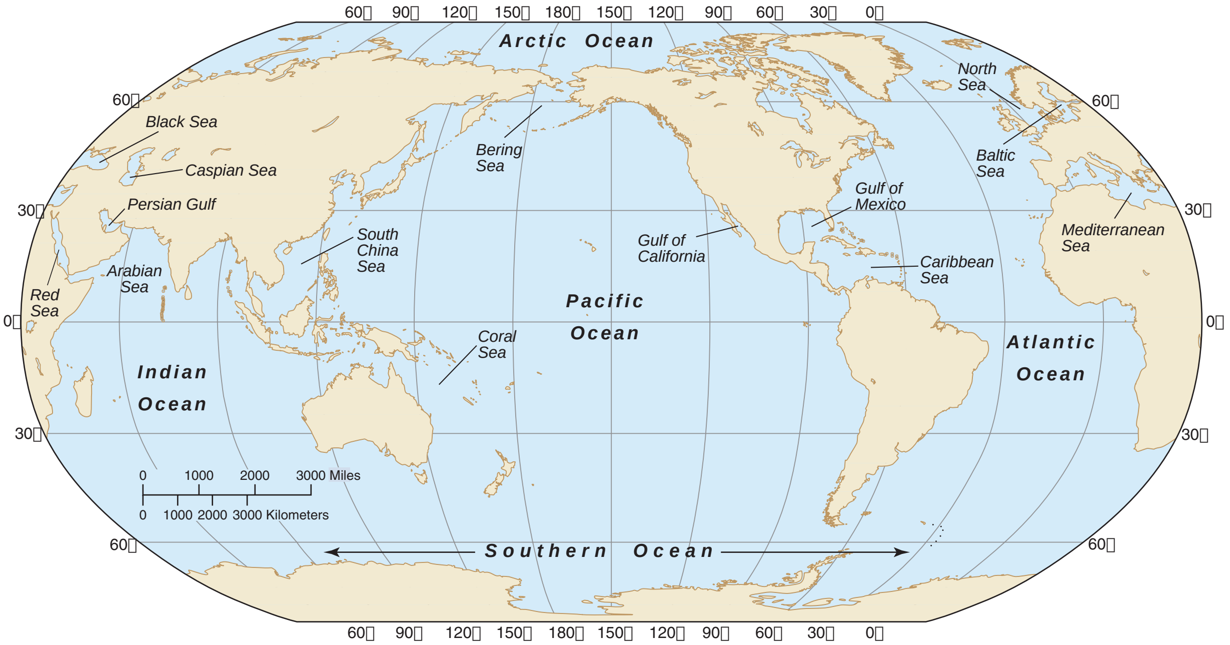

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
Arctic Ocean
North Sea
60°
Black Sea
Caspian Sea
Bering Sea
Baltic Sea
60°
30°
Persian Gulf
Gulf of Mexico
30°
South China Sea
Gulf of California
Mediterranean Sea
Arabian Sea
Caribbean Sea
Red Sea
Pacific Ocean
0°
0°
Coral Sea
Atlantic Ocean
Indian Ocean
30°
30°
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
60°
Southern Ocean
60°
60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°

FIGURE 2.1 The major ocean basins and some of the marginal seas.

The Geography of the Ocean Basins

The oceans are not distributed equally with respect to the Equator. About two-thirds of the earth's land area is found in the Northern Hemisphere, which is only 61% ocean. About 80% of the Southern Hemisphere is ocean.

The oceans are traditionally classified into four large basins (Fig. 2.1). The **Pacific** is the deepest and largest ocean, almost as large as all the others combined (Table 2.1). The **Atlantic** Ocean is a little larger than the **Indian** Ocean, but the two are similar in average depth. The **Arctic** is the smallest and shallowest ocean. A number of shallow seas, such as the Mediterranean Sea, Gulf of Mexico, and South China Sea, are connected or marginal to the main ocean basins.

Though we usually treat the oceans as four separate entities, they are actually interconnected. This connection is most obvious when the world is viewed from the South Pole (Fig. 2.2). From this view it is clear that the Pacific, Atlantic, and Indian oceans are large branches of one vast system. The connections among the major basins allow seawater, materials, and some organisms to move from one ocean to another. Because the oceans are actually one great interconnected system, oceanographers often speak of a single **world ocean.** They also refer to the continuous body of water that surrounds Antarctica as the **Southern Ocean.**

The world ocean, which covers 71% of the planet, is divided into four major basins: the Pacific, Atlantic, Indian, and Arctic oceans.

The Structure of the Earth

The earth and the rest of the solar system are thought to have originated about 4.5 billion years ago from a cloud or clouds of dust. This dust is thought to be the debris remaining from a great cosmic explosion called the **big bang,** which astrophysicists estimate occurred about 13.7 billion years ago. The dust particles collided with each other, clumping into larger particles. These larger particles collided in turn, joining into pebble-sized rocks that collided to form larger rocks, and so on. The process eventually built up the earth and other planets.

Table 2.1 Average Depths and Total Areas of the Four Major Ocean Basins

	AREA		AVERAGE DEPTH		
Ocean	**Millions of km^2**	**Millions of mi^2**	**Meters**	**Feet**	**Deepest Place**
Pacific	166.2	64.2	4,188	13,741	Mariana Trench, 11,022 m (36,163 ft)
Atlantic	86.5	33.4	3,736	12,258	Puerto Rico Trench, 8,605 m (28,233 ft)
Indian	73.4	28.3	3,872	12,704	Java Trench, 7,725 m (25,344 ft)
Arctic	9.5	3.7	1,330	4,364	Molloy Deep, 5,608 m (18,400 ft)

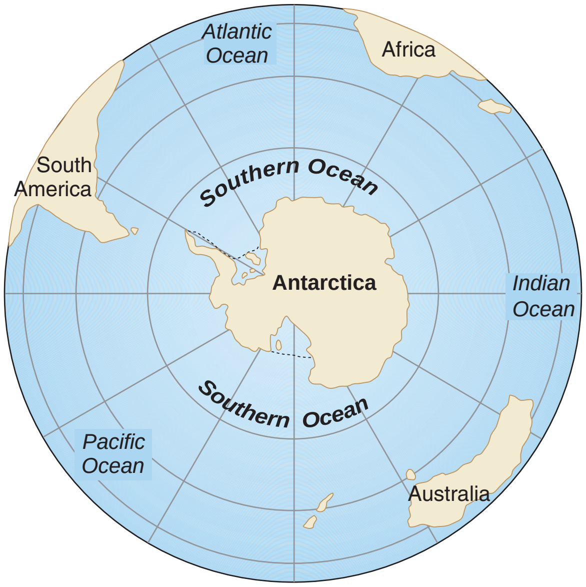


FIGURE 2.2 South polar view of the world. The major ocean basins can be seen as extensions of one interconnected world ocean. The ocean that surrounds Antarctica is often called the Southern Ocean.

So much heat was generated as the early earth formed that the planet was probably molten. This allowed materials to settle within the planet according to their **density.** Density is the mass of a given volume of a substance. Obviously, a pound of styrofoam weighs more than an ounce of lead, but most people think of lead as "heavier" than styrofoam. This is because lead weighs more than styrofoam if *equal volumes* of the two are compared. In other words, lead is denser than styrofoam. The density of a substance is calculated by dividing its mass by its volume. If two substances are mixed, the denser material tends to sink and the less dense to float.

Density is the mass of a substance per unit volume. Substances of low density will float on substances of higher density.

$$\text{density} = \frac{\text{mass}}{\text{volume}}$$

While the young earth was molten, the densest material tended to flow toward the center of the planet, while lighter materials floated toward the surface. The light surface material cooled into a thin crust. Eventually, the atmosphere and oceans began to form. If the earth had settled into orbit too far away from or too close to the sun, or our atmosphere had formed differently, the earth would be either so hot that all the water would have evaporated into space or so cold that all water on earth would be perpetually frozen. Fortunately for us, both our planet's orbit and its atmosphere are such that liquid water, and therefore life as we know it, can exist.

Internal Structure The internal structure of the earth reflects the planet's early beginnings. As materials sank or floated according to their density, they formed concentric layers like those of an onion (Fig. 2.3). The innermost layer, the **core,** is composed mostly of iron. The pressure in the core is more than a million times that at the earth's surface, and the temperature is estimated to be over 4,000°C (7,200°F). The core is made up of a solid inner core and a liquid outer core. It is thought that swirling motions of the liquid material in the iron-rich outer core produce the earth's magnetic field.

The layer outside the earth's core is the **mantle.** Though most of the mantle is thought to be solid, it is very hot—near the melting point of the rocks. Because of this, much of the mantle slowly flows almost like a liquid, swirling and mixing over hundreds of millions of years.

The **crust** is the outermost, and therefore best-known, layer of the earth. Compared with the deeper layers, it is extremely thin, like a rigid skin floating on top of the mantle. The composition and characteristics of the crust differ greatly between the oceans and the continents.

The earth is composed of three main layers: the iron-rich core, the semiplastic mantle, and the thin outer crust.

Continental and Oceanic Crusts The geological distinction between ocean and continents results from physical and chemical differences in the rock that makes up the crust (Table 2.2). The

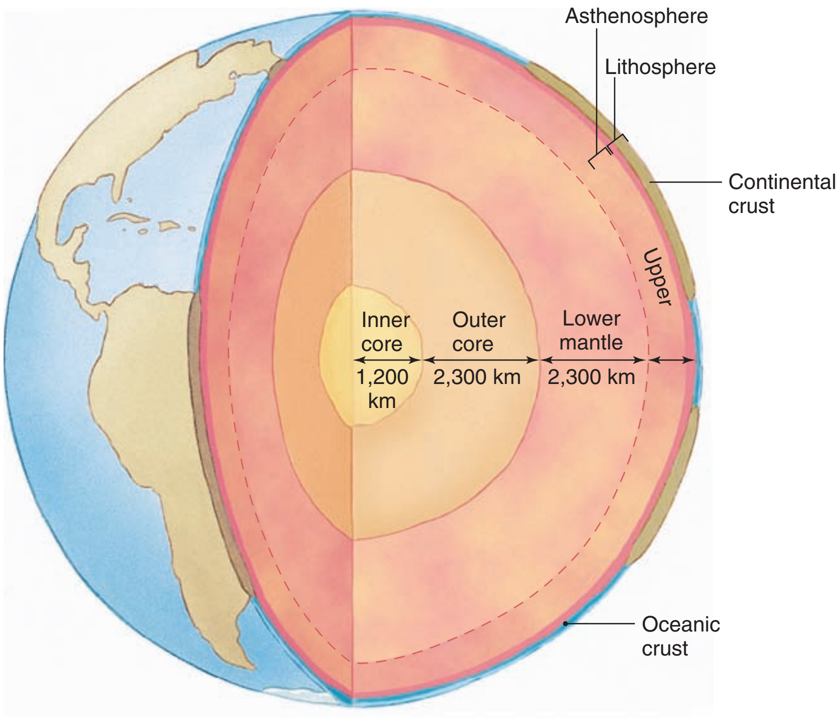


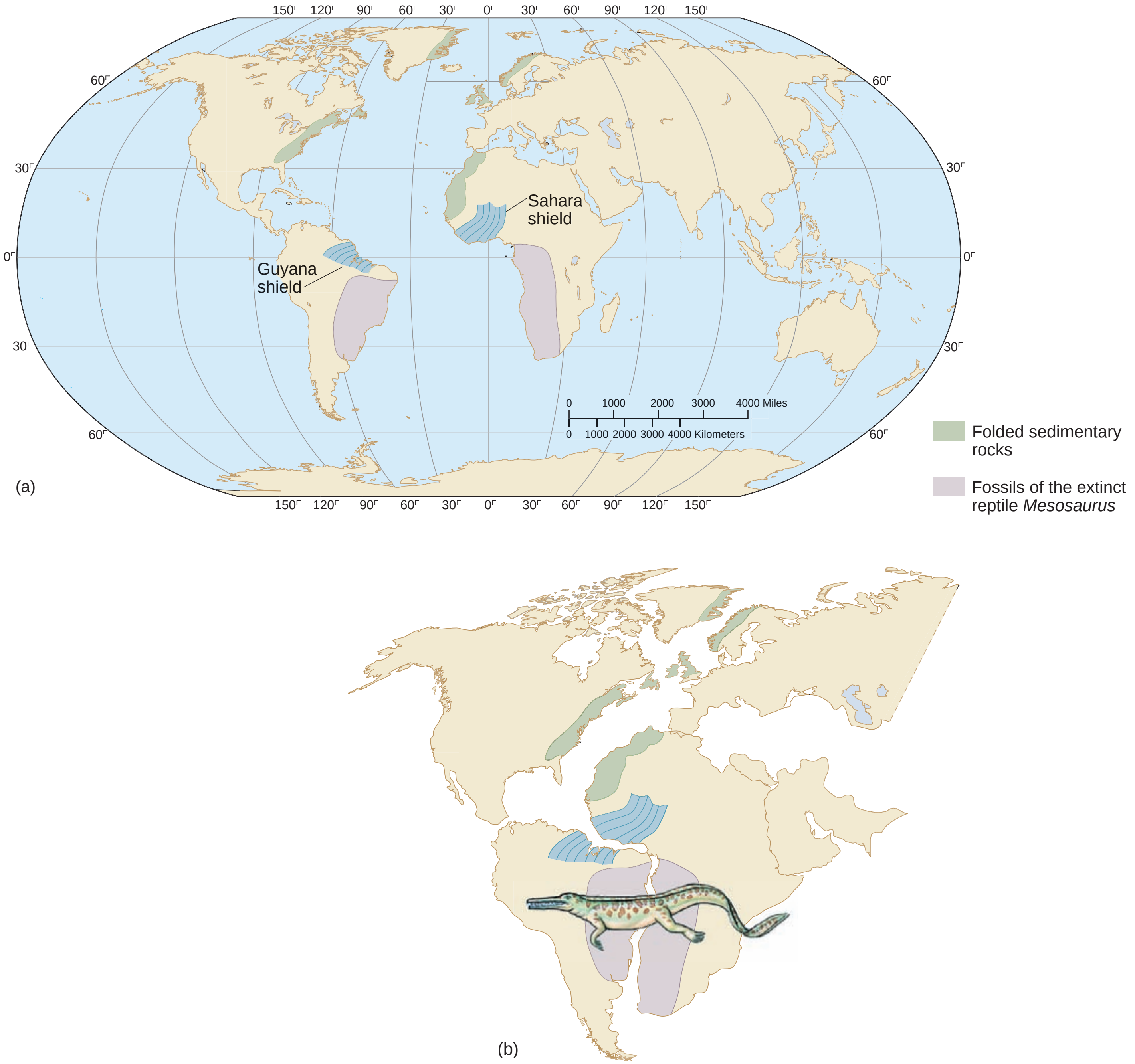
FIGURE 2.3 The interior of the earth is divided into the core, mantle, and crust. The core is subdivided into the solid inner core and the liquid outer core. The mantle is also subdivided into upper and lower layers. The very upper layer of the upper mantle is solid, and together with the crust forms the lithosphere. The upper mantle below the lithosphere is relatively fluid and is called the asthenosphere. The thickness of the crust and lithosphere is exaggerated here, and the thicknesses of all layers vary from place to place.

Table 2.2
Comparison of Continental and Oceanic Crusts

Oceanic Crust (Basalt)	Continental Crust (Granite)
Density about 3.0 g/cm^3	Density about 2.7 g/cm^3
Only about 5 km (3 mi) thick	20 to 50 km (12 to 30 mi) thick
Geologically young	Can be very old
Dark in color	Light in color
Rich in iron and magnesium	Rich in sodium, potassium, calcium, and aluminum

nature of the rock determines the elevation of a particular area of the earth's crust, and therefore whether or not it is covered by water.

Oceanic crust, which makes up the sea floor, consists of a type of mineral called **basalt** that has a dark color. Most continental rocks are of a general type called **granite,** which has a different chemical composition than basalt and is lighter in color. Oceanic crust is denser than continental crust, though both are less dense than the underlying mantle. The continents can be thought of as thick blocks of relatively light crust floating on the mantle, much as icebergs float in water. Oceanic crust floats on the mantle, too, but because it is denser it doesn't float as high.



150° 120° 90° 60° 30° 0° 30° 60° 90° 120° 150°
60°
30°
0°
30°
60°
Sahara shield
Guyana shield
0 1000 2000 3000 4000 Miles
0 1000 2000 3000 4000 Kilometers
(a)
Folded sedimentary rocks
Fossils of the extinct reptile *Mesosaurus*
(b)

FIGURE 2.4 (*a*) The landmasses on opposite sides of the Atlantic have coastlines and geological features that (*b*) fit together like pieces of a puzzle.

This is why the continents lie high and dry above sea level and oceanic crust lies below sea level, covered with water. Oceanic crust is also much thinner than continental crust.

Oceanic and continental crusts also differ in age. The oldest oceanic rocks are less than 200 million years old, quite young by geological standards. Continental rocks, on the other hand, can be as much as 3.8 billion years old.

THE ORIGIN AND STRUCTURE OF THE OCEAN BASINS

For centuries people viewed the world as static and unchanging. Evidence of geological change is all around, however, from catastrophic earthquakes and volcanic eruptions to the slow erosion of river valleys. People eventually understood that the face of the planet does indeed change. Today scientists recognize the earth as a world of constant transformation where even the continents move.

Early Evidence of Continental Drift

As early as 1620 the English philosopher, writer, and statesman Sir Francis Bacon noted that the coasts of the continents on opposite sides of the Atlantic fit together like pieces of a puzzle (Fig. 2.4). It was later suggested that the Western Hemisphere might once have been joined to Europe and Africa, and evidence for this slowly accumulated. Coal deposits and other geological formations, for example, match up on opposite sides of the Atlantic. Fossils collected on opposing coasts are also similar.

On the basis of such evidence Alfred Wegner, a German geophysicist, proposed the first detailed hypothesis of **continental drift** in 1912. Wegener suggested that all the continents had once been joined in a single "supercontinent," which he named **Pangaea.** He thought Pangaea began breaking up into the continents we know today about 180 million years ago.

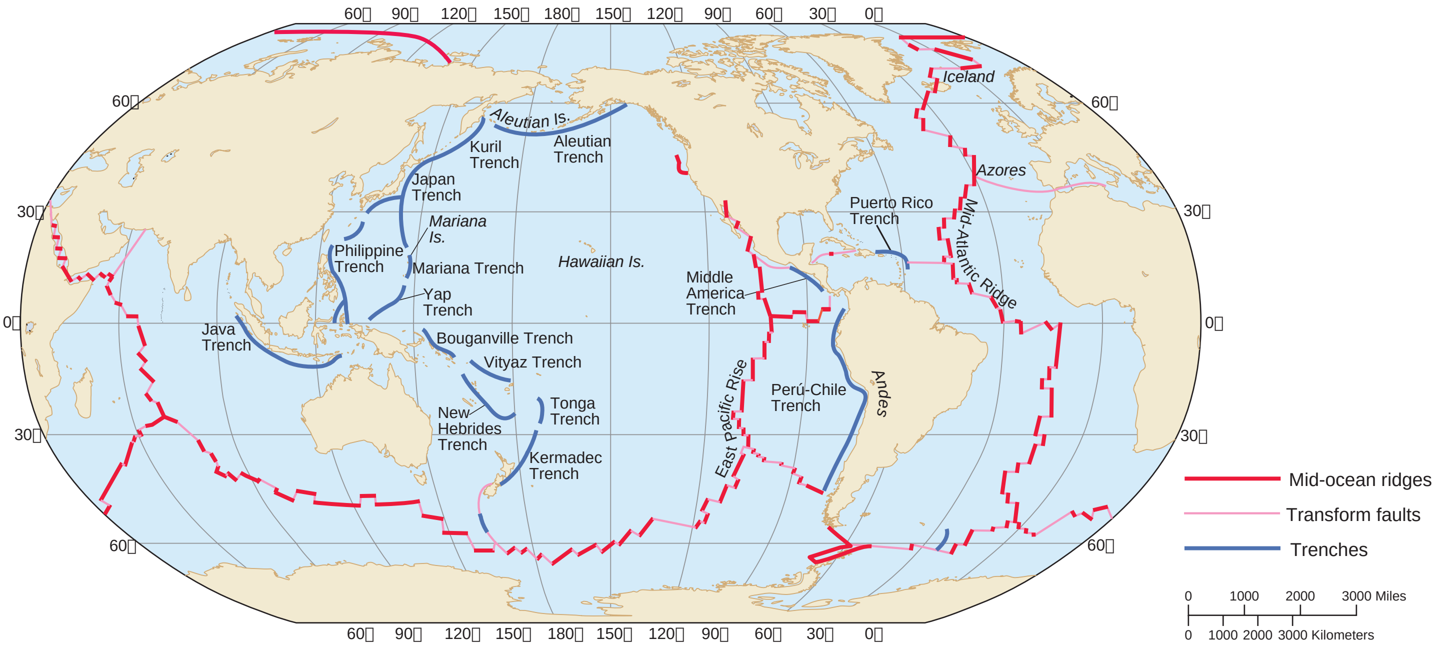
The Theory of Plate Tectonics

Wegener's hypothesis was not widely accepted because he could not explain *how* the continents moved. Later proposals of continental drift also failed to provide a workable mechanism, but evidence continued to accumulate. In the late 1950s and the 1960s scientists were able to put all the evidence together. They concluded that the continents *did* drift, as part of **plate tectonics,** a process that involves the entire surface of our planet.

Discovery of the Mid-Ocean Ridge In the years after World War II, sonar allowed the first detailed surveys of large areas of the sea floor. These surveys resulted in the discovery of the **mid-ocean ridge** system, a continuous chain of submarine volcanic mountains that encircles the globe like the seams on a baseball (Figs. 2.5 and 2.6). The mid-ocean ridge system is the largest geological feature on earth. At regular intervals the mid-ocean ridge is displaced to one side or the other by cracks, or **faults,** in the earth's crust known as **transform faults.** Occasionally the submarine mountains of the ridge rise so high that they break the surface to form islands, such as Iceland and the Azores.

The mid-ocean ridge in the Atlantic, called the **Mid-Atlantic Ridge,** runs right down the center of the Atlantic Ocean, closely following the curves of the opposing coastlines. The ridge forms an inverted Y in the Indian Ocean and runs up the eastern side of the Pacific (Fig. 2.5). The main section of ridge in the Eastern Pacific is called the **East Pacific Rise.**

The mid-ocean ridge system is a continuous, submarine range of volcanic mountains that runs through all the ocean basins.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60°
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0°
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60°
Iceland
Aleutian Is.
Kuril Trench
Aleutian Trench
Japan Trench
Azores
Mariana Is.
Puerto Rico Trench
Mid-Atlantic Ridge
Philippine Trench
Mariana Trench
Hawaiian Is.
Middle America Trench
Yap Trench
Java Trench
Bouganville Trench
Vityaz Trench
East Pacific Rise
Perú-Chile Trench
Andes
Tonga Trench
New Hebrides Trench
Kermadec Trench
Mid-ocean ridges
Transform faults
Trenches
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers

FIGURE 2.5 The major features of the sea floor. Compare this map with Figure 2.6.

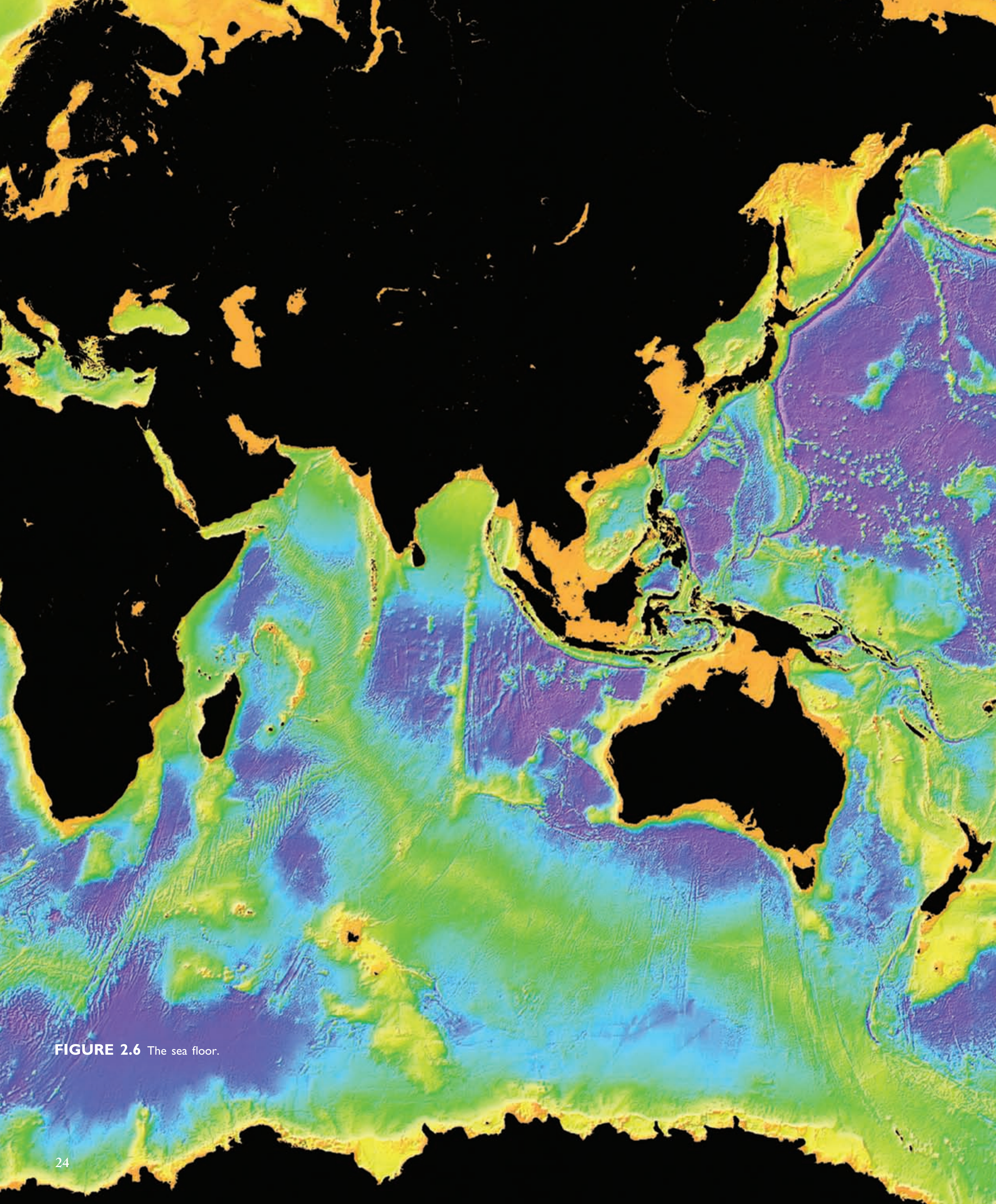
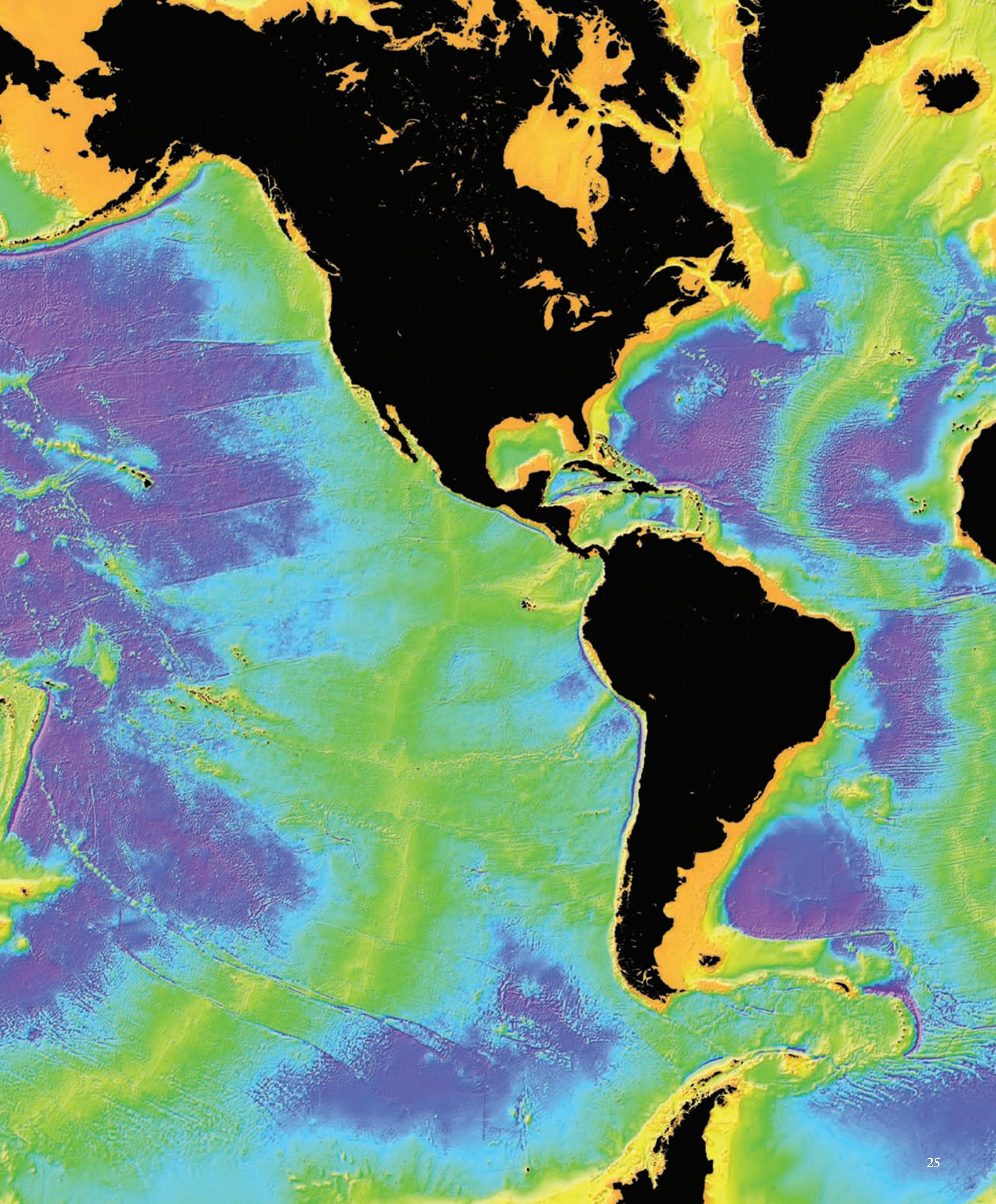


FIGURE 2.6 The sea floor.



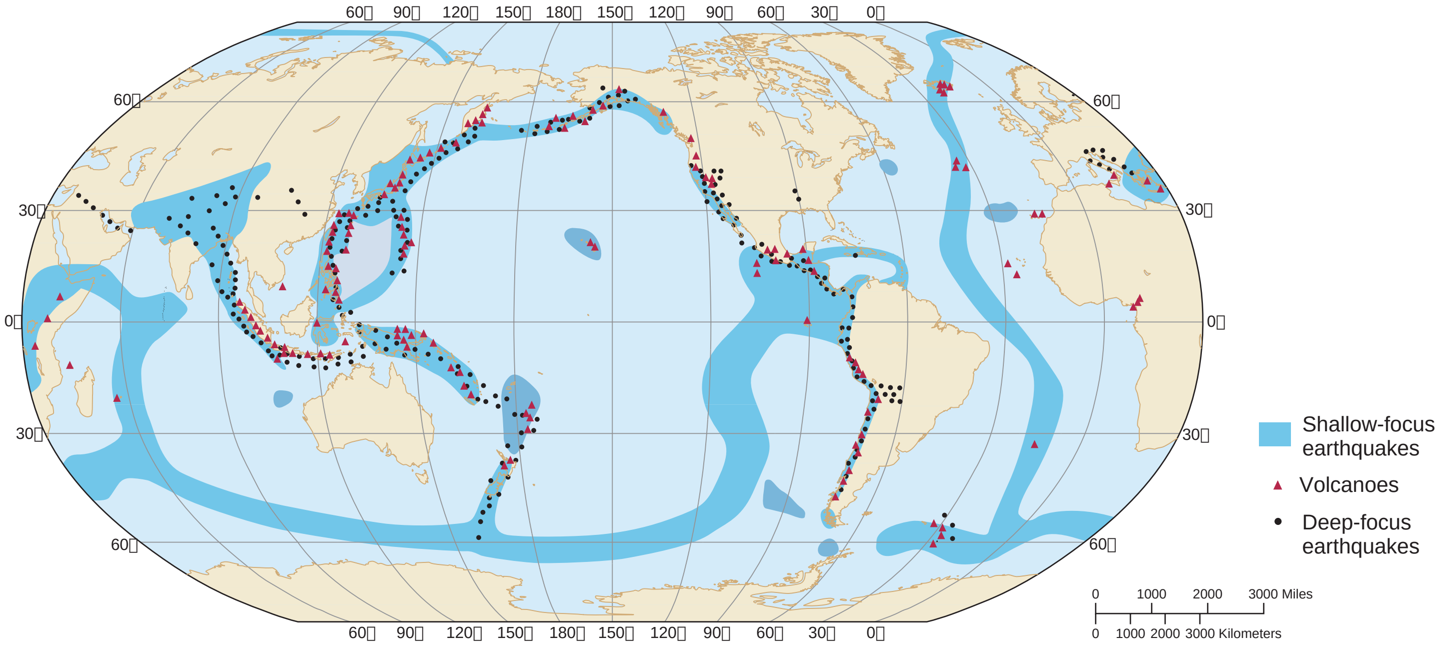


FIGURE 2.7 The world distribution of earthquakes and volcanoes. Compare these with the locations of mid-ocean ridges and trenches shown in Figure 2.5.

Surveys of the sea floor also revealed the existence of a system of deep depressions in the sea floor called **trenches** (Fig. 2.5). Trenches are especially common in the Pacific. How they are formed is discussed in "Sea-Floor Spreading and Plate Tectonics," (p. 27).

Significance of the Mid-Ocean Ridge When the mid-ocean ridge system and trenches were discovered, geologists realized that geological activity is concentrated around these features. Earthquakes are clustered at the ridge, for example, and volcanoes are associated with trenches (Fig. 2.7).

The nature of the sea floor is also related to the mid-ocean ridge. Sea-floor rock at the ridge is very young, and gets progressively older moving away from the ridge. Right at the ridge crest there is little if any **sediment,** loose material like sand and mud that settles to the bottom, but sediments get thicker and thicker at greater distance from the ridge. The deepest sediment, that resting directly on the sea-floor rock, gets older away from the ridge.

One of the most important findings came from studying the magnetism of rocks on the sea floor. The earth's magnetic field periodically reverses direction. When a magnetic compass points north as it does today the magnetic field is arbitrarily called "normal." During a reversal the field is opposite that of today and the compass would point south. These reversals happen about every 700,000 years on average, but the interval may be less than 100,000 years or tens of millions. It takes about 5,000 years for the field to reverse itself, quite sudden by geological standards. The cause of the reversals is thought to be related to movements of material in the earth's molten outer core.

Many rocks contain tiny magnetic particles. When the rock is molten these particles are free to move and act like tiny compasses, pointing north or south depending on whether the earth's field is normal or reversed. When the rocks cool, the particles are frozen in place and keep their orientation even when the magnetic field changes. It is therefore possible to tell the orientation of the earth's magnetic field at the time the rocks cooled.

Sea-floor rocks have patterns of magnetic bands, or "stripes," that run parallel to the mid-ocean ridge (Fig. 2.8). The bands represent zones in which the rocks alternate between normal and reversed magnetization. The bands are symmetric around the ridge, so that the pattern on one side of the ridge is a mirror image of the pattern on the other side. These bands, or **magnetic anomalies,** could only have formed if the normally magnetized rock cooled from molten material at different times than the reverse-magnetized bands. The sea floor, then, was not formed all at once but in strips that parallel the mid-ocean ridge.

Earthquakes and volcanoes are associated with the mid-ocean ridge. The sediments are thicker and the rock of the actual sea floor is older the farther they are from the ridge. Bands of rock alternating between normal and reversed magnetism parallel the ridge.

Creation of the Sea Floor The discovery of magnetic anomalies, together with the other evidence, finally led to an understanding of plate tectonics. The jump from the various observations of the sea floor and mid-ocean ridges to the theory of plate tectonics is a good example of the use of **induction** in science.

Huge pieces of oceanic crust are separating at the mid-ocean ridges, creating cracks in the crust called **rifts.** When a rift occurs it releases some of the pressure on the underlying mantle, like

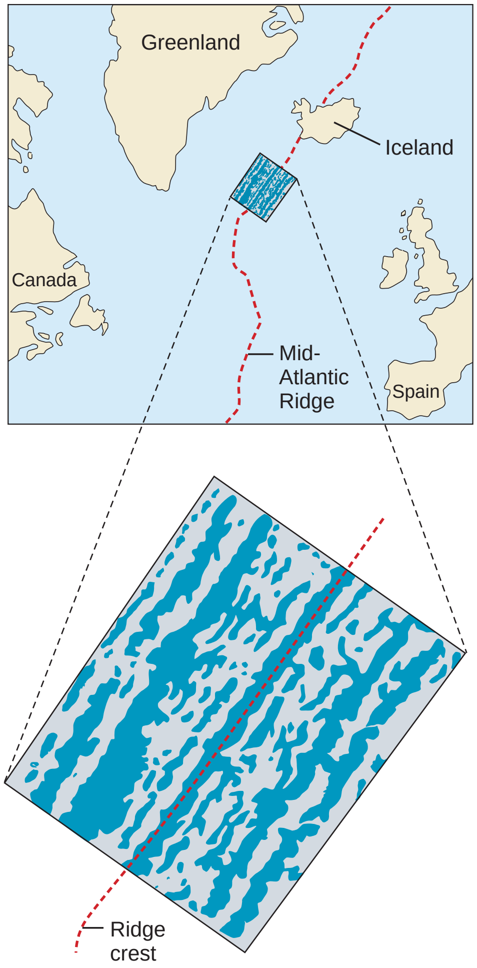


FIGURE 2.8 Rocks with normal magnetization cooled from molten rocks at a time when the earth's magnetic field was "normal," that is, the same as it is today. If the positions of sea-floor rocks with normal (dark) and reversed (light) magnetization are drawn on a map, they form bands running parallel to the mid-ocean ridge. Note that the rocks at the ridge crest have normal magnetization.

removing the cap from a bottle of soda pop. The reduced pressure allows hot mantle material to melt and rise up through the rift. The ascending mantle material, or magma, pushes up the oceanic crust around the rift to form the mid-ocean ridge (Fig. 2.9). When this molten material reaches the earth's surface it cools and solidifies to form new oceanic crust. The process repeats itself as the sea floor continues to move away from the mid-ocean ridge. The entire process by which the sea floor moves away from the mid-ocean ridges to create new sea floor is called **sea-floor spreading,** and the ridges are also called spreading centers.

Sea-floor spreading explains many observations related to the mid-ocean ridge. Right at the ridge crest the crust is new and has not had time to accumulate a layer of sediment. As the crust moves away from the ridge it ages and sediment builds up. This explains why the sediment gets thicker and the rocks get older as one moves away from the ridge. Sea-floor spreading also explains the pattern of magnetic stripes. As new sea floor is created, it freezes the magnetic field prevailing at the time and preserves that magnetization as it moves away from the ridge. Eventually the earth's magnetic field reverses, starting a new stripe.

Sea-Floor Spreading and Plate Tectonics Sea-floor spreading is only part of the story of plate tectonics. The earth's surface is covered by a fairly rigid layer composed of the crust and the uppermost part of the mantle. This layer, averaging about 100 km (60 mi) thick, is called the **lithosphere,** meaning "rock sphere" (see Fig. 2.3). The lithosphere is broken into a number of plates called **lithospheric plates** (Fig. 2.10). A plate can contain continental crust, oceanic crust, or both. The lithosphere floats on a denser, more plastic layer of the upper mantle called the **asthenosphere.** While the crust, mantle, and core are distinguished by their chemical composition, the distinction between the lithosphere and the asthenosphere is based on how easily the rock flows.

The earth's surface is broken up into a number of plates. These plates, composed of the crust and the top part of the mantle, make up the lithosphere. The plates are about 100 km (60 mi) thick.

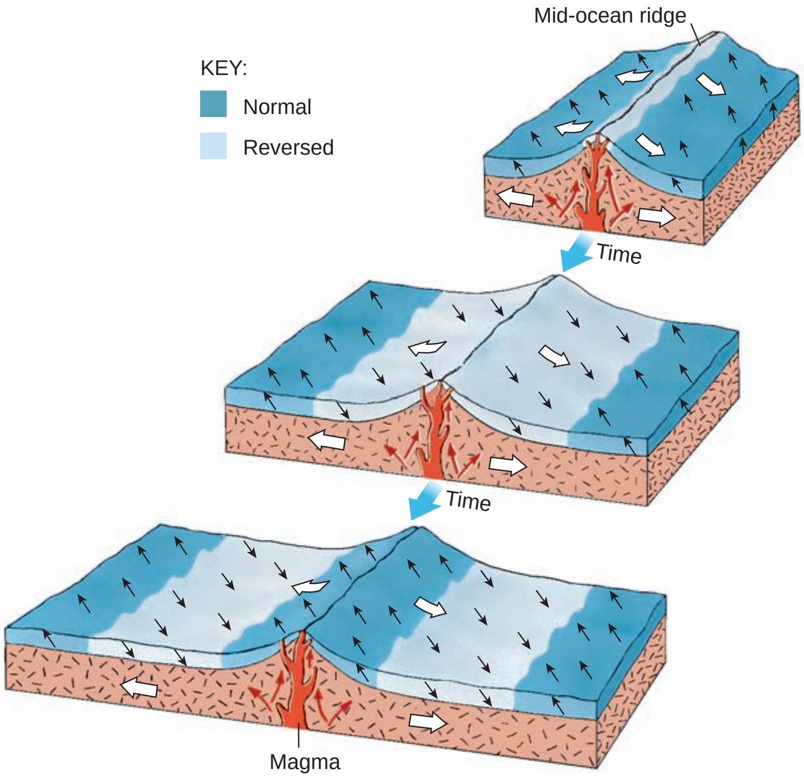


FIGURE 2.9 Cross section of the sea floor at a mid-ocean ridge showing the mechanism of sea-floor spreading. As the sea floor moves away from the rift, molten material rises from the mantle and cools to form new sea floor. When the rocks cool, they "freeze" whatever magnetic orientation, normal or reversed, is present at the time. The entire floor of the ocean was created at the mid-ocean ridge in this manner.

Induction The development of a generalized conclusion from a series of individual observations.

- Chapter 1, p. 9

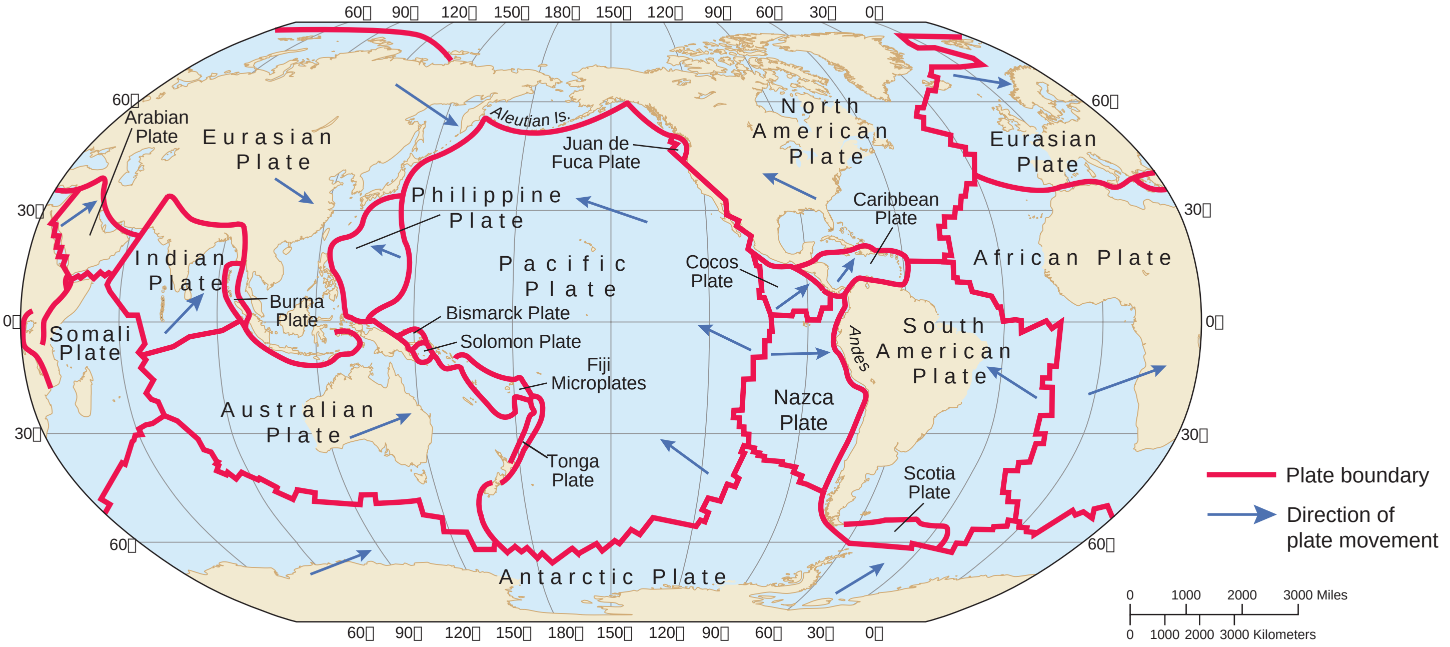

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60°
30°
0°
30°
60°
Arabian Plate
Eurasian Plate
Aleutian Is.
Juan de Fuca Plate
North American Plate
Eurasian Plate
Philippine Plate
Caribbean Plate
Indian Plate
Pacific Plate
Cocos Plate
African Plate
Burma Plate
Bismarck Plate
Somali Plate
Solomon Plate
South American Plate
Andes
Fiji Microplates
Nazca Plate
Australian Plate
Tonga Plate
Scotia Plate
Antarctic Plate
Plate boundary
Direction of plate movement
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers

FIGURE 2.10 The division of the earth's surface into lithospheric plates. Some areas are not fully understood, and there are some small plates not shown here. Compare this map with those in Figures 2.5 and 2.7.

Mid-ocean ridges form the edges of many of the plates. Here the lithospheric plates move apart and new sea floor—that is, new oceanic lithosphere—is created by sea-floor spreading. If the plate includes a block of continental crust, the continent is carried along with the plate as it moves away from the ridge. This is the mechanism of continental drift. The plates spread at around 2 to 18 cm (0.8 to 7 in) per year. For comparison, human fingernails grow at about 6 cm (2.4 in) per year. The spreading rate varies from place to place and over time.

As new lithosphere is created, old lithosphere is destroyed somewhere else. Otherwise, the earth would have to expand constantly to make room for the new lithosphere. Lithosphere is destroyed at trenches, which are another important type of boundary between plates. A trench is formed when two plates collide and one of the plates dips below the other and sinks back down into the mantle (Figs. 2.11 and 2.12). This downward movement of the plate into the mantle is called **subduction,** and trenches are also called **subduction zones.**

As the plate sinks, it weakens under the heat and pressure of the mantle and begins to break up, causing earthquakes. Eventually the plate gets so hot it melts. Some of the molten material rises back to the surface to form volcanoes. The rest continues to sink into the mantle. Some of this material may eventually be recycled, rising again at another mid-ocean ridge several hundred million years later.

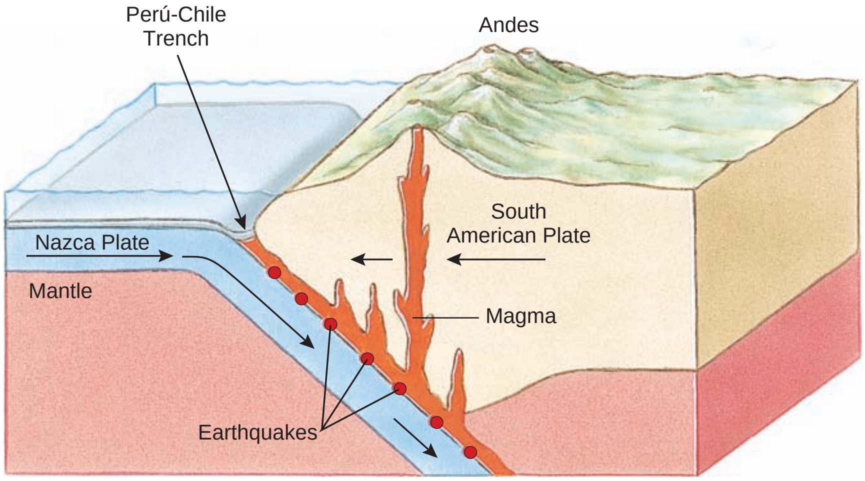

Perú-Chile Trench
Andes
South American Plate
Nazca Plate
Mantle
Magma
Earthquakes

FIGURE 2.11 Some trenches are formed by the collision of continental and oceanic plates. In this example the Nazca Plate dips beneath the South American Plate. Earthquakes are produced as the Nazca Plate descends into the mantle. The lighter materials from the sinking plate rise back to the surface as they melt, creating the volcanic Andes (see Figs. 2.5, 2.6, and 2.7).

At trenches a lithospheric plate descends into the mantle, where it breaks up and melts. This process, called subduction, produces earthquakes and volcanoes.

The collision that produces a trench can be either between an oceanic plate and a continent or between two oceanic plates. When an oceanic plate collides with a continent, it is always the oceanic plate that descends into the mantle. This is because the continental block is less dense than the oceanic plate and floats on top. This is why very old rocks are found only on the continents: Because oceanic crust is eventually destroyed at trenches, it never gets old by geological standards. Continental crust, on the other hand, is not destroyed in trenches and can last for billions of years.

A collision between oceanic and continental plates causes the development of continental volcanoes associated with the trench. These volcanoes may form coastal mountain ranges. The Andes on the Pacific coast of South America are a good example of this (Fig. 2.11).

The oceanic plate lifts the edge of the continent slightly when it slides down under the continent. As the slab of cold lithosphere sinks deeper in the mantle, however, it tends to drag the interior of the continent down with it. The central part of the continent subsides, sometimes so much that seawater floods in to form shallow seas. After tens of millions of years the continent breaks free of the sinking plate and floats back up to its normal elevation, and the shallow sea disappears. This is thought to have occurred in North America when a huge slab of oceanic lithosphere called the Farallon Plate slid under the west coast. That explains why Denver, Colorado, the "mile-high city," is surrounded by rocks formed from marine sediments.

When two oceanic plates collide, one of the plates dips beneath the other to form the trench. Again the trench is associated with earthquakes and volcanoes (Figs. 2.12 and 2.13). The volcanoes may rise from the sea floor to create chains of volcanic islands. As viewed on a map, trenches are curved because of the earth's spherical shape. The volcanic island chains associated with the trenches follow the trenches' curvature and are called **island arcs.** Examples include the Aleutian and Mariana islands (see Figs. 2.5 and 2.6).

Occasionally two continental plates collide. Because of the relatively low density of continental crust, both plates tend to float and neither is subducted. Therefore, no trench is formed. Instead, the two continental blocks push against each other with such tremendous force that the two continents become "welded" together. The force is eventually too much for the rocks, which buckle and fold like an accordion. The huge folds form mountain ranges. The Himalayas, for example, were formed when India collided with the rest of Asia (see "Continental Drift and the Changing Oceans," p. 30).

There is a third type of plate boundary in addition to trenches and mid-ocean ridges. Sometimes two plates move in such a way that they slide past each other, neither creating nor destroying lithosphere. This type of plate boundary is called a **shear boundary.** In the fault where the two plates move past each other there is immense friction between the plates. This friction prevents the plates from sliding smoothly. Instead they lock, and stress builds up until the plates break free and slip all at once, causing an earthquake. The San Andreas Fault in California is the largest and most famous example of a shear boundary (Fig. 2.14).

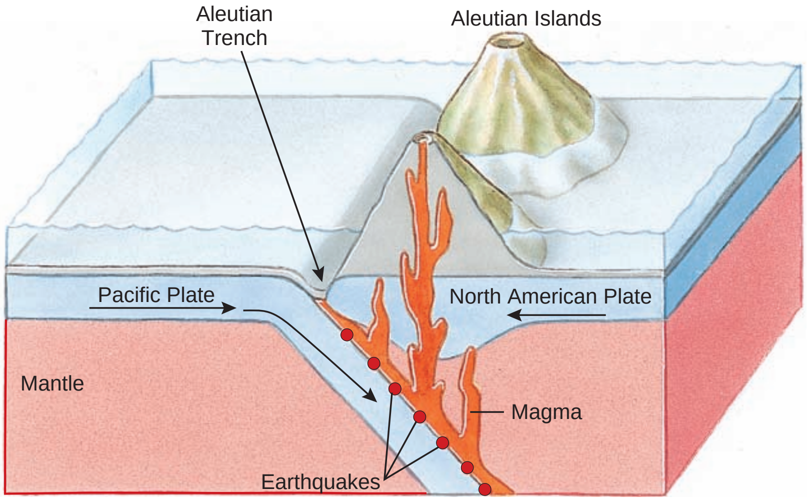


FIGURE 2.12 Trenches can also be caused by the collision of two oceanic plates. The oceanic portion of the North American Plate has collided with the Pacific Plate. In this case, the Pacific Plate dipped below the North American Plate, but either of the two plates might have done so. Earthquakes are produced by the descending plate. The volcanoes associated with the trench have produced the Aleutian Island arc (see Figs. 2.5, 2.6, and 2.7).

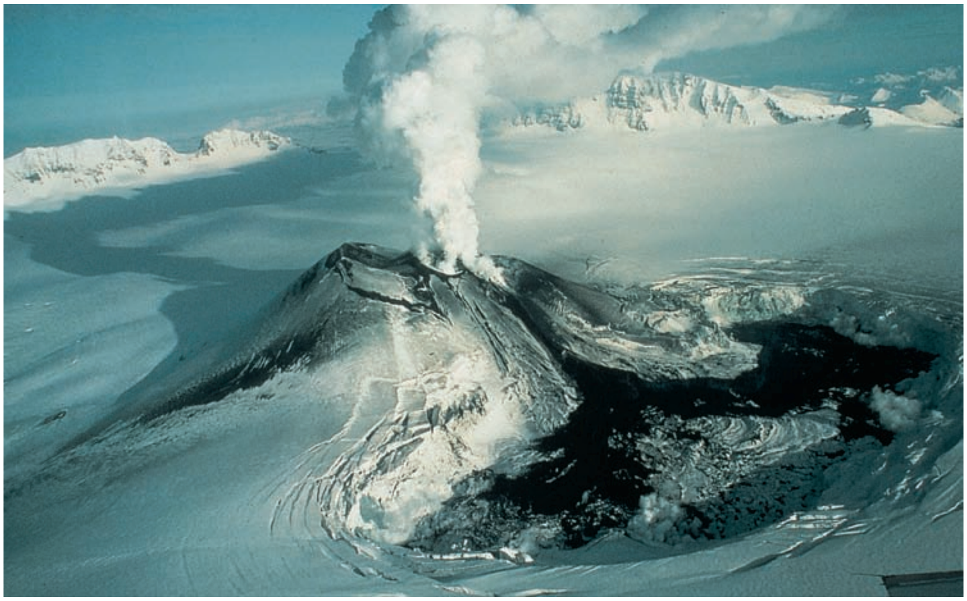


FIGURE 2.13 Mount Veniaminof, an active volcano on the Alaska Peninsula. Geologically, the Alaska Peninsula is part of the Aleutian Island chain that has formed behind the Aleutian Trench (see Figs. 2.5 and 2.12).

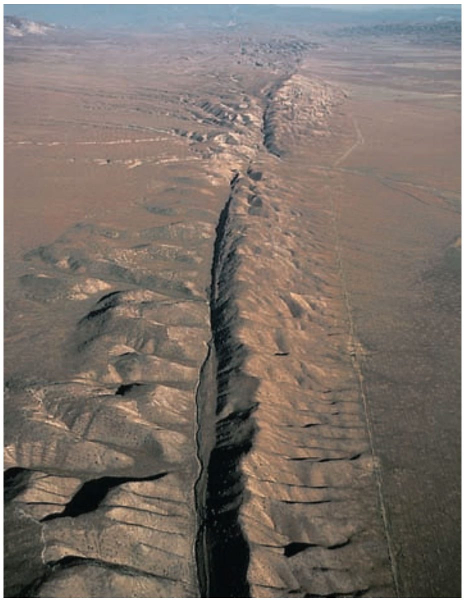


FIGURE 2.14 The San Andreas Fault on the Carrizo Plain, California.

EYE ON SCIENCE

Deep-Ocean Drilling

When mid-ocean ridges, trenches, and magnetic anomalies were discovered, geologists clamored for actual *samples* of the sea floor that they could hold in their hands and analyze in their labs. The ship *Glomar Challenger* was purpose-built for the technologically daunting task of drilling core samples from the deep-sea floor and began operation in 1968. In 1985 a new and improved drill ship, *JOIDES Resolution,* took over. In nearly four decades, the two ships drilled over 3,000 holes in the sea floor, recovering more than 35,000 sediment and rock samples. The samples revolutionized our understanding of the sea floor, the ocean, and the entire planet. Early samples confirmed sea-floor spreading by the increasing age of rocks moving away from the ridges, their magnetism, and other features of the sea floor. Drilling still provides vital new information about plate tectonics and the structure of the earth, but it also supports many other studies. Ocean drilling discovered microbes living in rocks 800 m (2,600 ft) below the sea floor, provides microfossils and other clues to past climate and ocean circulation (see "The Record in the Sediments," p. 32), helps us better understand and perhaps eventually predict earthquakes, helped put a date on when the Himalayas were born, and revealed a characteristic, worldwide sediment layer that is probably the signature of the asteroid collision 65 million years ago that wiped out the dinosaurs. In December 2005, scientists aboard *JOIDES Resolution* achieved a 40-year goal by drilling deep in the crust into a fossil magma chamber to obtain rock samples that are expected to help determine exactly how new oceanic crust is formed from cooled mantle material.

Immediately after this breakthrough, *JOIDES Resolution* went into port for a badly needed upgrade. She was scheduled to sail again in late 2007, and be joined by a new Japanese drill ship, *Chikyu* (meaning "Earth"). *Chikyu* was designed to drill deep enough to achieve geologists' long-time dream of penetrating the mantle itself, and she can drill in both shallower and deeper water than *JOIDES Resolution. Chikyu* can also work in the poorly explored Arctic Ocean (with a little help from icebreakers).

Unfortunately, there have been snags in these ambitious plans. High oil prices and a boom in oil exploration led to a spike in demand for, and the cost of, drilling equipment, blowing out the budget for *JOIDES Resolution's* refit. Meanwhile, *Chikyu* was damaged in a sudden storm during a shakedown cruise and has run into budget problems of her own. To meet rising costs, *Chikyu's* schedule has been changed to take on commercial oil exploration tasks. Despite these setbacks, scientists are confident that deep-ocean drilling will get through the tough times and embark on a new wave of discoveries.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

Geologists once thought the most likely explanation for what makes the plates move was **convection,** in which heat from the earth's core causes the mantle to swirl like thick soup heating in a saucepan. It was thought that the convection currents carry the overlying plates along like icebergs in a current (Fig. 2.15). Since the 1990s, however, more and more geologists have come to the view that mantle convection is probably not the main cause of plate motion. The most widely accepted hypothesis today is that oceanic lithosphere cools as it ages, becoming denser. Eventually it sinks into the mantle, forming a trench and pulling the rest of the plate along behind it. This "slab pull" causes the plates to separate at the mid-ocean ridge, allowing fresh magma to well up from the mantle. Convection may still have a role in plate motion, and the upwelling mantle material may also help push the plates apart.

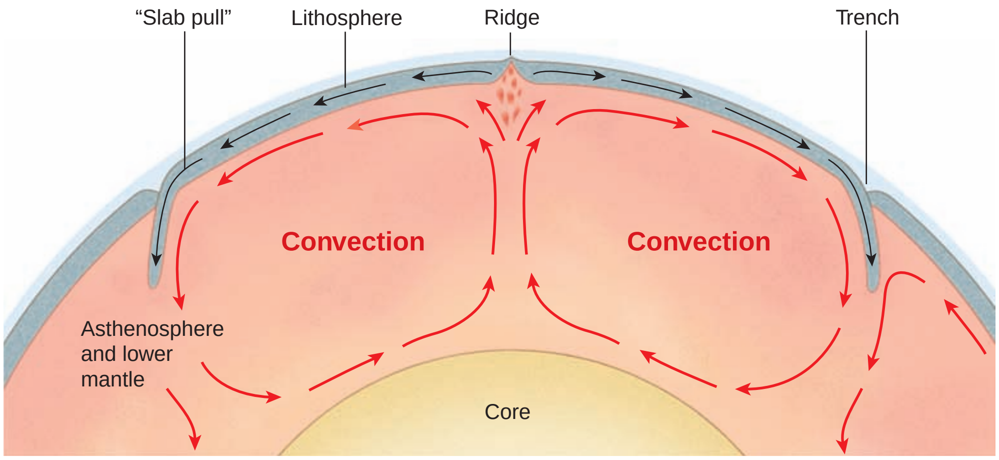
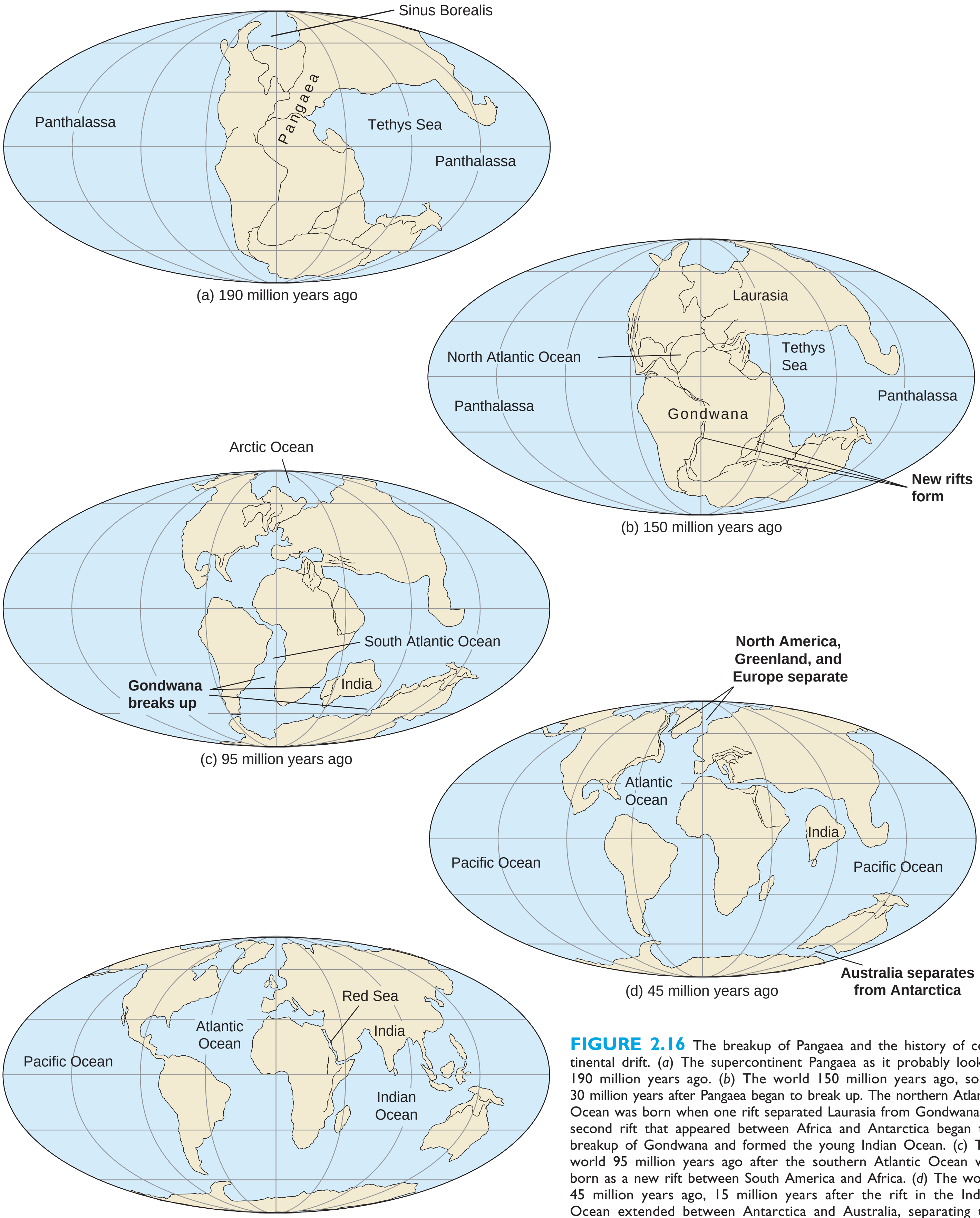


FIGURE 2.15 The movement of lithospheric plates was long thought to be driven by large-scale convection currents in the asthenosphere and lower mantle, driven in turn by heat from the earth's core. Mantle convection is much more complex than shown here, however, and today the prevailing hypothesis is that the plates move mainly because of slab pull, in which old, cold, and dense lithosphere sinks into the mantle and pulls the rest of the plate behind it. It may be this sinking cold rock rather than heat from the core that stirs the mantle.

The Geological History of the Earth

Whatever drives plate tectonics, we know that the earth's surface has undergone dramatic alterations. The continents have been carried long distances by the moving sea floor, and the ocean basins have changed in size and shape. In fact, new oceans have been born.

Continental Drift and the Changing Oceans About 200 million years ago all the continents were joined in the supercontinent Pangaea, just as Wegener proposed. Antarctica was in approximately the same place it is today, but all the other continents were in different positions (Fig. 2.16*a*). India was attached to Antarctica and Africa rather than to Eurasia as it is now.


Sinus Borealis
Pangaea
Panthalassa
Tethys Sea
Panthalassa
Laurasia
North Atlantic Ocean
Tethys Sea
Panthalassa
Panthalassa
Gondwana
New rifts form
Arctic Ocean
South Atlantic Ocean
Gondwana breaks up
India
North America, Greenland, and Europe separate
Atlantic Ocean
India
Pacific Ocean
Pacific Ocean
Australia separates from Antarctica
Red Sea
India
Atlantic Ocean
Pacific Ocean
Indian Ocean

(a) 190 million years ago

(b) 150 million years ago

(c) 95 million years ago

(d) 45 million years ago

(e) 15 million years ago

FIGURE 2.16 The breakup of Pangaea and the history of continental drift. (*a*) The supercontinent Pangaea as it probably looked 190 million years ago. (*b*) The world 150 million years ago, some 30 million years after Pangaea began to break up. The northern Atlantic Ocean was born when one rift separated Laurasia from Gondwana. A second rift that appeared between Africa and Antarctica began the breakup of Gondwana and formed the young Indian Ocean. (*c*) The world 95 million years ago after the southern Atlantic Ocean was born as a new rift between South America and Africa. (*d*) The world 45 million years ago, 15 million years after the rift in the Indian Ocean extended between Antarctica and Australia, separating the two continents. (*e*) The world about 15 million years ago.

Pangaea was surrounded by a single, vast ocean called **Panthalassa.** Panthalassa, which covered all the rest of the planet, was the ancestor of the modern Pacific Ocean. A relatively shallow sea, the **Tethys Sea,** separated Eurasia from Africa. The Tethys Sea, the precursor of the present-day Mediterranean, was home to many of the world's shallow-water organisms. Another indentation in the coast of Pangaea, the Sinus Borealis, was to become the Arctic Ocean. Before Pangaea began to break up, there was no sign of the modern Atlantic or Indian oceans.

Approximately 180 million years ago, a new rift appeared between North America and the combined continents of South America and Africa (Fig. 2.16*b*). This rift was the beginning of the Mid-Atlantic Ridge, and its formation marked the birth of the North Atlantic Ocean. Pangaea was now separated into two large continents. One was **Laurasia,** composed of what is now North America and Eurasia. South America, Africa, Antarctica, India, and Australia made up the southern continent of **Gondwana.**

At around the same time another rift began to split up Gondwana, marking the beginning of the Indian Ocean. South America and Africa began to move to the northeast, and India, separated from the other continents, began to move north.

About 135 million years ago the South Atlantic was born when a new rift occurred between South America and Africa (Fig. 2.16*c*). This rift eventually joined the mid-ocean ridge in the North Atlantic to form a single mid-ocean ridge. As the Atlantic Ocean grew, the Americas were carried away from Eurasia and Africa. To make room for the new sea floor produced in the Atlantic, the Pacific Ocean—the descendant of Panthalassa—steadily shrank. The Atlantic is still growing, and the Pacific shrinking.

The Y-shaped ridge that produced the Indian Ocean gradually extended to separate Australia from Antarctica (Fig. 2.16*d*). The base of the inverted Y extended into the African continent, forming the Red Sea, which is actually a young ocean. India continued to move north until it collided with Asia (Fig. 2.16*e*) to create the Himalayas. The Tethys Sea closed up and disappeared as Africa, and then India, moved up into Asia. Most of the organisms that once lived in the Tethys Sea are now known only as fossils, although the descendants of a few surviving species still live in the Caspian, Black, and Mediterranean Seas.

The continents were once united in a single supercontinent called Pangaea that began to break up about 180 million years ago. The continents have since moved to their present positions.

The breakup of Pangaea to form today's continents is only the most recent turn of a continuing cycle. For hundreds of millions of years the continents have been adrift. They alternately collide and re-form into larger landmasses, only to break up and drift apart again.

The Record in the Sediments We have already seen how the increase in sediment thickness moving away from mid-ocean ridges gave a clue to how plate tectonics works. Marine sediments provide a wealth of other information about the earth's past. The type of sediment laid down on the sea floor often reflects the prevailing conditions in the ocean above. By studying sediments that were deposited in the past, oceanographers have learned a great deal about the history of the planet.

Most marine sediments are of two basic types. The first is **lithogenous sediment,** which is derived from the physical and chemical breakdown, or **weathering,** of rocks, mostly on the continents. Coarse sediments, which consist of relatively large particles, tend to sink to the bottom rapidly rather than being carried out to sea by ocean currents (see "The Shifting Sediments," p. 259). Coarse lithogenous sediments, therefore, are usually deposited near the edges of the continents. Finer material sinks much more slowly and is carried far out to sea by currents. Some fine material is even transported as dust by the wind. The most common kind of lithogenous sediment on the open ocean floor is a fine sediment called **red clay.**

The second major type of marine sediment, **biogenous sediment,** consists of the skeletons and shells of marine organisms, including **diatoms, radiolarians, foraminiferans,** and **coccolithophorids.** Some biogenous sediments are composed of the mineral **calcium carbonate ($CaCO_3$).** This type of sediment is called **calcareous ooze.** The other type of biogenous sediment is made of **silica (SiO_2),** which is similar to glass. It is called **siliceous ooze.**

The two most abundant types of marine sediment are lithogenous sediment, which comes from the weathering of rocks on land, and biogenous sediment, which is composed of the remains of marine organisms. Biogenous sediment is made mostly of calcium carbonate or silica.

Though large fossils like whale bones and shark teeth can be found, most of the organisms that produce biogenous sediments are microscopic or nearly so. Such sediment particles are sometimes called **microfossils,** since each particle represents the preserved remains of a dead organism (Fig. 2.17). Microfossils tell scientists what organisms lived in the ocean in the past. Because some of these organisms are known to prefer cold or warm water, microfossils also give clues to ancient ocean temperatures. Ocean temperatures are determined by the earth's climate and ocean currents.

The climate of the earth in the past can also be determined by the chemical composition of the microfossils. Various methods including **carbon dating,** a procedure in which the ratios of different atomic forms, or **isotopes,** of carbon are measured, can be

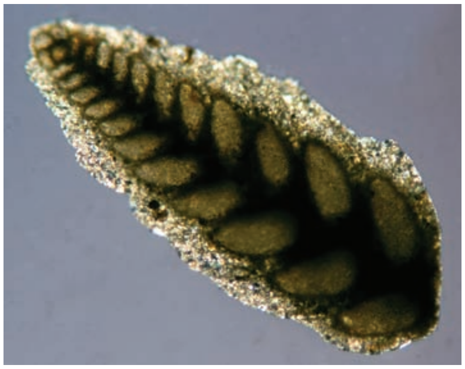


FIGURE 2.17 The fossil shell of a foraminiferan *(Textularia).*

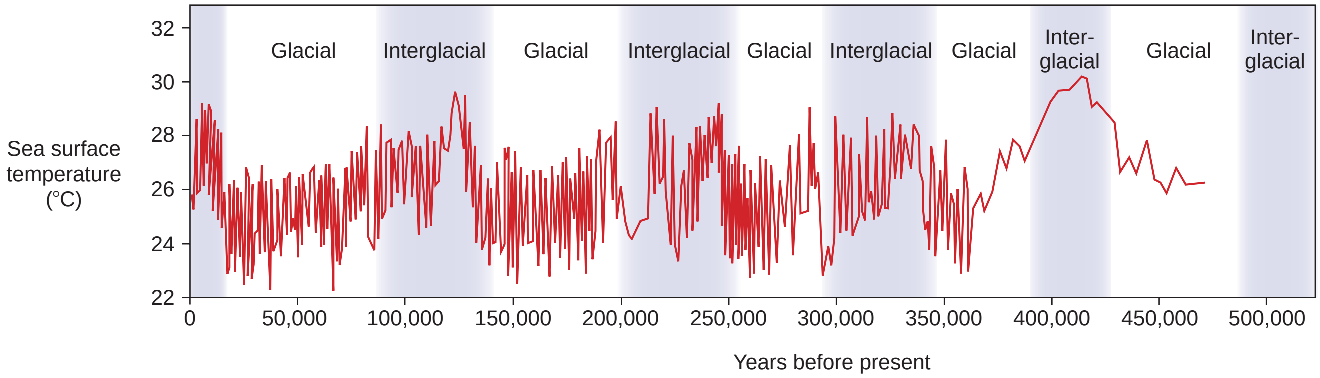


FIGURE 2.18 A history of the earth's climate over the past half-million years as determined from foraminiferan microfossils. The red line shows the average sea surface temperature in the equatorial Pacific Ocean as determined from the magnesium-to-calcium ratio in the microfossils. The white and blue bands indicate major glacial and interglacial periods, respectively, recorded in oxygen isotope ratios. Note that the shifts between ice ages and interglacial periods involve relatively small changes in average temperature.

used to determine the age of microfossils. It is also possible to tell the temperature of the water in which the organisms lived by measuring the ratios of magnesium (Mg) to calcium (Ca) or of different isotopes of oxygen in the microfossils. Thus, microfossils have preserved a detailed record of the earth's past climate. Though the record in the sediments is not always easy to read, it is supplemented by other information. The ratio of the elements strontium (Sr) and calcium in ancient coral skeletons, for example, also records past ocean temperatures. Ice cores from polar areas like Greenland and Antartica also preserve a record of past temperatures, as well as samples of the ancient atmosphere in the form of tiny bubbles trapped in the ice. These and other studies are providing an increasingly detailed picture of the earth's past climate (see "Rolling the Dice: Climate Change," p. 231).

Climate and Changes in Sea Level The climate of the earth has fluctuated rhythmically through much of its history, alternating between warm, or **interglacial,** periods and cold periods, or **ice ages** (Fig. 2.18). The earth is presently in an interglacial period. During ice ages, great glaciers build up on the continents. Because large amounts of water are trapped as ice instead of flowing to the sea in rivers, there is less water in the ocean. Thus, sea level falls during ice ages.

The **Pleistocene Epoch,** which began a little less than 2 million years ago, was the last major period of glaciation. During the Pleistocene a series of ice ages was interspersed by brief warm periods of melting. The peak of the last ice age occurred about 18,000 years ago. At that time, vast ice sheets as thick as 3 km (2 mi) covered much of North America and Europe. Sea level was about 130 m (425 ft) lower than it is today.

Sea level falls during ice ages because water is trapped in glaciers on the continents. The last major ice age occurred about 18,000 years ago.

Sea level continues to rise, though the rate of melting slowed during the past 3,000 years. Some scientists think that without the influence of humans the earth would be entering another ice age. Human impact on the atmosphere, however, has intensified the **greenhouse effect.** Global temperatures and the rate of glacial melting are now increasing, and sea level is projected to continue to rise for at least the next century (see "Special Report: Our Changing Planet," p. 231).

THE GEOLOGICAL PROVINCES OF THE OCEAN

The structure of the ocean floor is dominated by the workings of plate tectonics. Because this is a global process, the major features of the sea floor are quite similar from place to place around the world. The sea floor is divided into two main regions: the **continental margins,** which represent the submerged edges of the continents, and the deep-sea floor itself.

Continental Margins

The continental margins are the boundaries between continental crust and oceanic crust. Most of the sediment from the continents settles to the bottom soon after reaching the sea and accumulates on the continental margins. Sediment deposits on the continental margins may be as thick as 10 km (6 mi). Continental margins generally consist of a shallow, gently sloping **continental shelf,** a steeper **continental slope** seaward of the continental shelf, and another gently sloping region, the **continental rise,** at the base of the continental slope (Fig. 2.19).

Diatoms Single-celled algae with a shell, or test, made of silica.
- Chapter 5, p. 94; Figure 5.6

Coccolithophorids Single-celled algae covered with plates made of calcium carbonate.
- Chapter 5, p. 97; Figure 5.10

Foraminiferans (Forams) Protozoans, often microscopic, with a calcium carbonate shell.
- Chapter 5, p. 97; Figure 5.11

Radiolarians Single-celled protozoans with a test made of silica.
- Chapter 5, p. 98; Figure 5.12

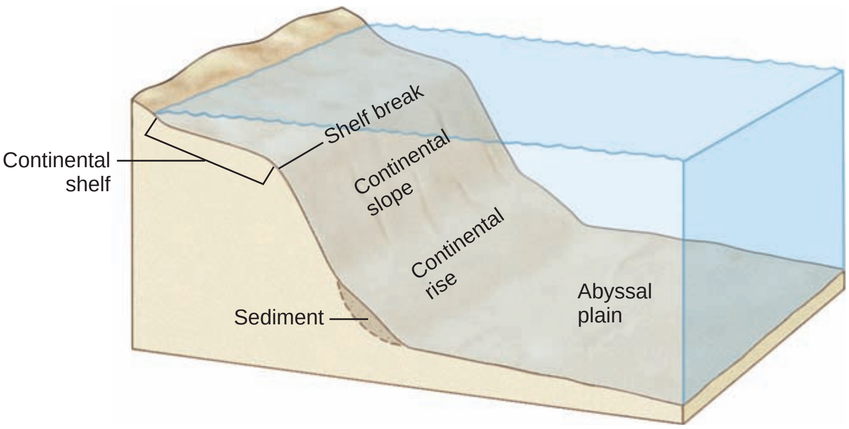


FIGURE 2.19 An idealized continental margin consists of a continental shelf, continental slope, and a continental rise. Seaward of the continental rise lies the deep-sea floor, or abyssal plain. These basic features vary from place to place.

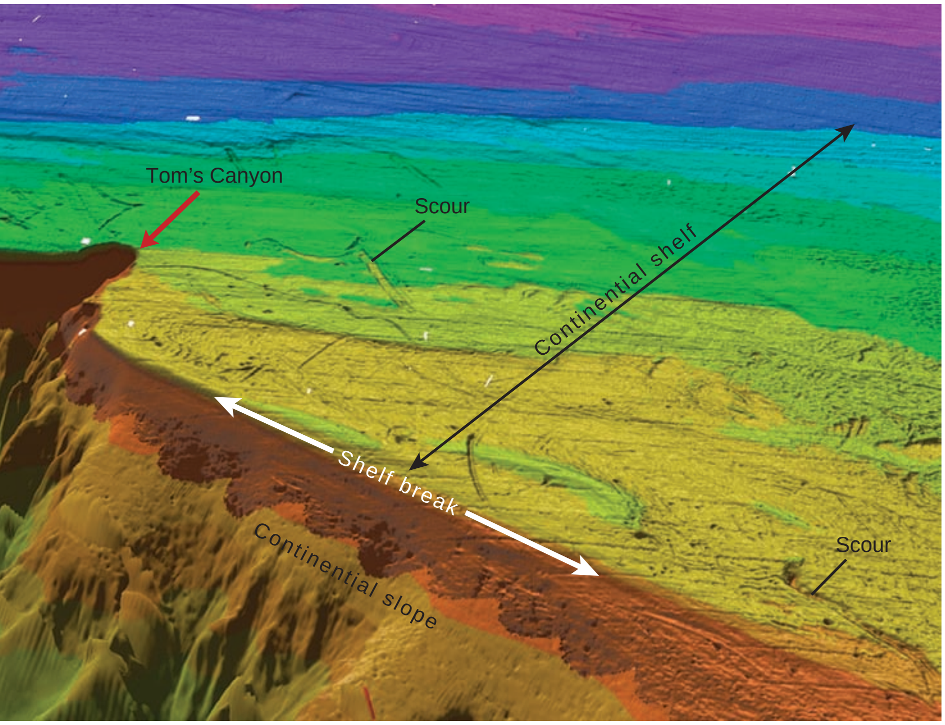
The Continental Shelf The shallowest part of the continental margin is the continental shelf. Though they make up only about 8% of the ocean's surface area, continental shelves are the biologically richest part of the ocean, with the most life and the best fishing. The shelf is composed of continental crust and is really just part of the continent that presently happens to be under water. During past times of low sea level, in fact, most of the continental shelves were exposed. At these times, rivers and glaciers flowed across the continental shelves and eroded deep canyons. When sea level rose, these canyons were submerged and gave rise to much larger **submarine canyons.**

The continental shelf extends outward at a gentle slope that in most places is too gradual to see with the naked eye. The shelf varies in width from less than 1 km (0.6 mi) on the Pacific coast of South America and other places to more than 750 km (470 mi) on the Arctic coast of Siberia. The continental shelf ends at the **shelf break,** where the slope abruptly gets steeper (Fig. 2.20). The shelf break usually occurs at depths of 120 to 200 m (400 to 600 ft) but can be as deep as 400 m (1,300 ft).

The Continental Slope The continental slope is the closest thing to the exact edge of the continent. It begins at the shelf break and descends downward to the deep-sea floor. Submarine canyons beginning on the continental shelf cut across the continental slope to its base at a depth of 3,000 to 5,000 m (10,000 to 16,500 ft; Fig. 2.21). These canyons channel sediments from the continental shelf to the deep-sea floor.

The Continental Rise Sediment moving down a submarine canyon accumulates at the canyon's base in a deposit called a **deep-sea fan,** similar to a river delta. Adjacent deep-sea fans may merge to form the continental rise. The rise consists of a thick layer of sediment piled up on the sea floor. Sediment may also be carried along the base of the slope by currents, extending the continental rise away from the deep-sea fans.

FIGURE 2.20 A section of the continental shelf (upper right) off Atlantic City, New Jersey, approximately 30 km (19 mi) wide. The white arrows indicate the shelf break. The red arrow shows the head of a submarine canyon called Tom's Canyon. The linear marks on the shelf are iceberg scours made during the last ice age. This image was created with a sophisticated form of sonar known as multibeam sonar. The steepness of the continental slope is exaggerated.



Continental margins have three main parts. The continental shelf is the submerged part of the continent and is almost flat. The relatively steep continental slope is the actual edge of the continent. The continental rise is formed by sediments building up on the sea floor at the base of the continental slope.

Active and Passive Margins The nature of the continental margin, and therefore of the biological habitats on the coast, depends to a large extent on the plate tectonic processes occurring in the region. The continent of South America provides a good example of the relationship between the continental margin and plate tectonics (Fig. 2.22). The South American Plate (see Fig. 2.10) consists of both the continent itself and the part of the Atlantic sea floor created by the Mid-Atlantic Ridge. South America is carried westward along with the plate as new sea floor is created in the Atlantic. The west coast of South America is colliding with the Nazca Plate, leading to the creation of a trench (see Figs. 2.5 and 2.11). Trenches are zones of intense geological activity, including earthquakes and volcanoes, so this type of continental margin is called an **active margin.** The west coast of North America also has a type of active margin, but it is much more complex than that of South America.

As the colliding plate descends into the trench, some of the sediment gets scraped off, folded, and "plastered" onto the continental margin. The edge of the continent is lifted by the oceanic plate passing below (see "Sea-Floor Spreading and Plate Tectonics," p. 27), and the coast is built up by volcanoes. These processes give active margins steep, rocky shorelines (Fig. 2.23), narrow continental shelves, and steep continental slopes. Because the sediments at the base of the continental slope are either carried down into the trench or scraped onto the continent, active margins usually lack a well-developed continental rise.

South America's east coast, on the other hand, is not a boundary between plates and is therefore relatively inactive geologically. The continental margin here can be thought of as the trailing edge left when South America separated from Africa. This type of margin is called a **passive margin.** Passive margins typically have flat

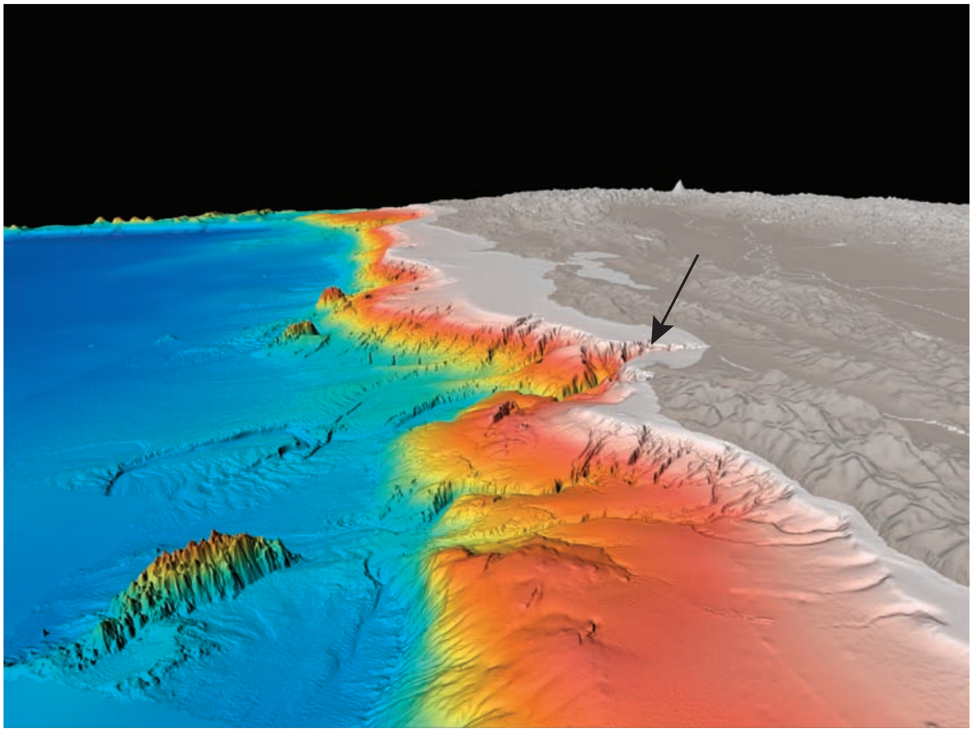


FIGURE 2.21 Multibeam sonar image of the continental margin off California. A number of submarine canyons cut across the continental shelf and down the continental slope to the deep-sea floor. The largest is Monterey Canyon, which extends nearly to the shore at Monterey Bay (arrow).

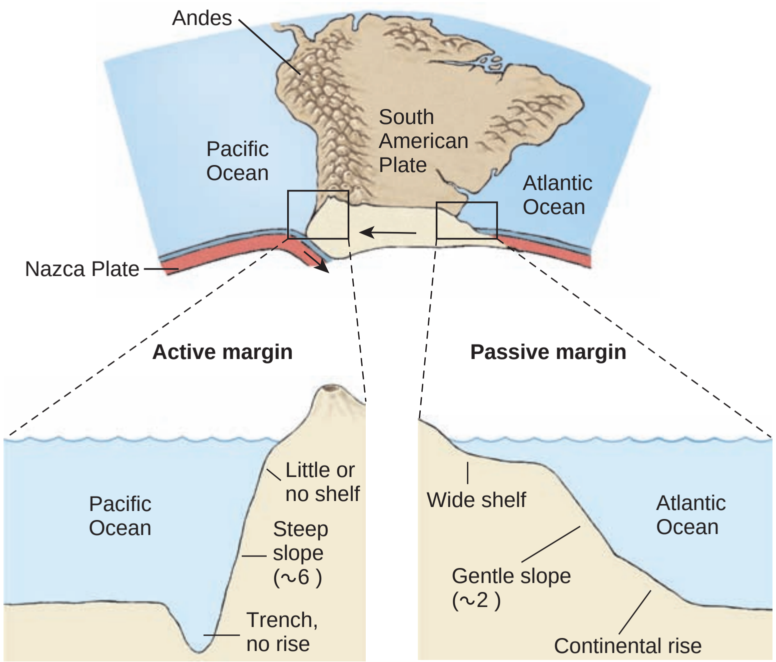


FIGURE 2.22 The opposite sides of South America have very different continental margins. The leading edge, or west coast, is colliding with the Nazca Plate. It has a narrow shelf and steep slope and has a trench rather than a continental rise. The trailing edge—that is, the Atlantic coast—has a wide shelf, a relatively gentle continental slope, and a well-developed continental rise. The steepness of all the slopes is exaggerated for illustrative purposes. Compare this with the map in Figure 2.5.

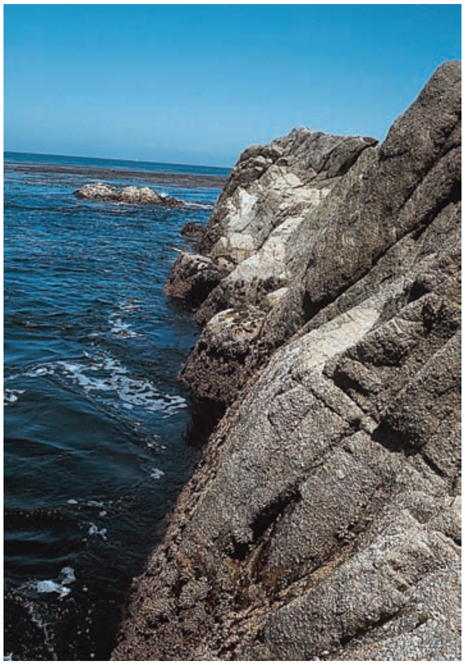
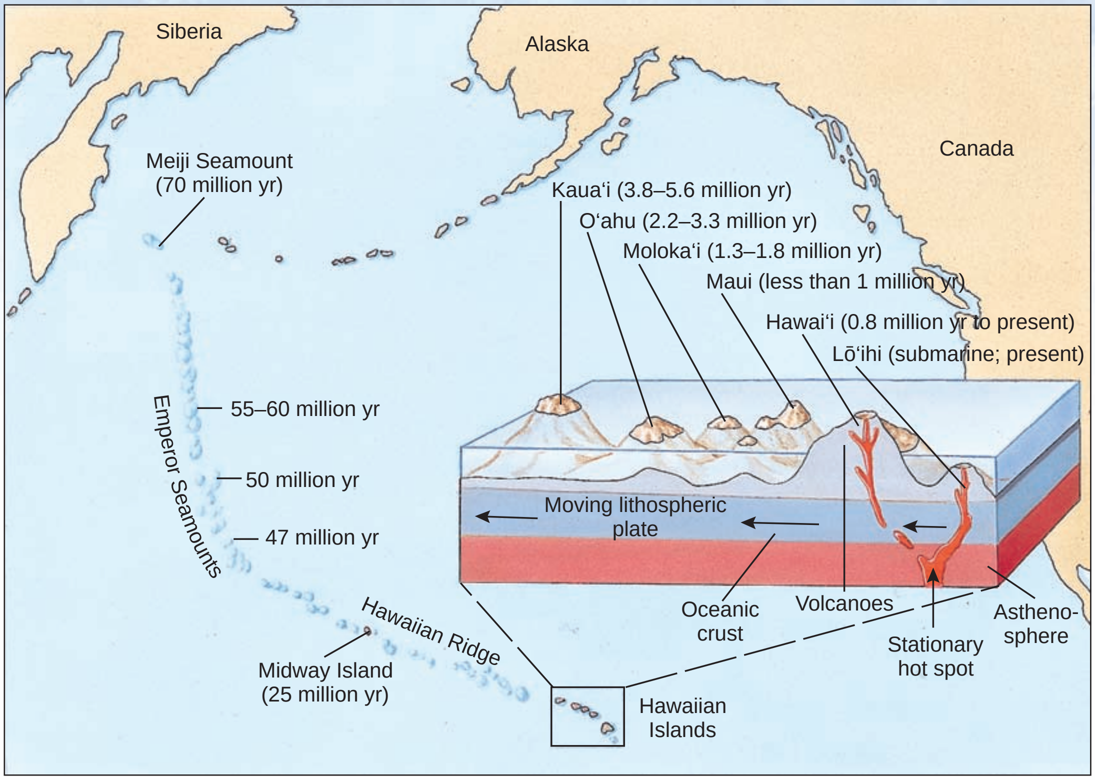


FIGURE 2.23 Steep, rocky shorelines like this one along the Pacific coast of North America at Monterey, Bay, California, are typical of active margins, although they occur in other places. The special problems of the organisms living on shores like this are discussed in Chapter 11.

The Hawaiian Islands, Hot Spots, and the Great Mantle Plume Debate


Siberia
Alaska
Canada
Meiji Seamount (70 million yr)
Kaua‘i (3.8–5.6 million yr)
O‘ahu (2.2–3.3 million yr)
Moloka‘i (1.3–1.8 million yr)
Maui (less than 1 million yr)
Hawai‘i (0.8 million yr to present)
Lō‘ihi (submarine; present)
55–60 million yr
50 million yr
47 million yr
Emperor Seamounts
Moving lithospheric plate
Oceanic crust
Volcanoes
Astheno-sphere
Stationary hot spot
Hawaiian Ridge
Midway Island (25 million yr)
Hawaiian Islands

The Emperor Seamounts and Hawaiian Island chain. Some geologists think that the chain was formed not by a hot spot as shown here but by a crack in the lithosphere.

The Hawaiian Islands are part of a chain of volcanoes called the Hawaiian Ridge, which is connected to a string of seamounts stretching to the northwest called the Emperor Seamount chain. The volcanoes get progressively older along the chain. A young submarine volcano called Lō‘ihi lies southeast of the island of Hawai‘i, the youngest Hawaiian island, and could grow into a new island. Hawai‘i began forming less than a million years ago and is still erupting. Much of the island is bare volcanic rock too young to have eroded or for vegetation to grow. Kaua‘i, at more than 5 million years old, is the oldest of the main Hawaiian Islands. It is densely vegetated, and erosion has

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coastal plains (Fig. 2.24), wide shelves, and relatively gradual continental slopes. Because there are no tectonic processes to remove it, sediment accumulates at the base of the continental slope. Passive margins therefore usually have a thick continental rise.

FIGURE 2.24 The Atlantic coast of North America has a passive margin. Because of the lack of geological activity and the buildup of sediments, most of the eastern seaboard has a broad coastal plain, with barrier islands, salt marshes, lagoons, and estuaries.

Active continental margins have narrow shelves, steep slopes, and little or no continental rise. Passive margins have wide shelves, relatively gentle slopes, and a well-developed rise.

Deep-Ocean Basins

Most of the deep-sea floor lies at a depth of 3,000 to 5,000 m (10,000 to 16,500 ft), averaging about 4,000 m (13,000 ft). The deep-sea floor, or **abyssal plain,** rises at a very gentle slope of less than 1 degree toward the mid-ocean ridge. Though relatively flat, it often has submarine channels, low **abyssal hills,** plateaus, rises, and other features. The abyssal plain is dotted with volcanic islands and submarine volcanoes called **seamounts.** Distinctive flattopped seamounts called **guyots** (pronounced "*gee*-ohs") are common in parts of the Pacific. Guyots and many other seamounts were once islands, but are now several hundred meters beneath the sea surface

Volcanic eruption at Kilauea, Hawai'i.

produced steep, jagged cliffs. The remaining islands and seamounts of the chain continue to get older moving to the northwest. Midway, about two-thirds of the way up the Hawaiian Ridge, is about 25 million years old. Meiji Seamount, at the northernmost end of the chain, is 70 million years old.

This pattern is widely attributed to a hot spot, a place where a plume of hot magma rises from deep in the mantle and forces its way through the lithosphere to erupt in volcanic activity. As the Pacific Plate moves over the stationary hot spot, each new eruption of magma breaks out at a slightly different place, producing the line of volcanoes. The bend between the Hawaiian Ridge and the Emperor Seamounts is thought to have occurred when the Pacific Plate changed direction.

Geologists have identified around 50 other hot spots around the world. Most are under oceanic plates. Hot spots are credited for other island-seamount chains in the Pacific Ocean; the Gilbert and Tokelau chains even have bends like the Hawaiian-Emperor chain. Hot spots associated with mid-ocean ridges and hence not under moving plates are thought to have created single islands or groups of islands rather than chains. Examples include Iceland, the Azores, and the Galápagos Islands. There are also a few hot spots beneath continents. The most famous is associated with the geysers and bubbling pools of Yellowstone and a line of progressively older volcanoes to the northwest. Geologists hypothesize that even larger masses of hot magma called superplumes also rise from deep in the mantle, lifting up great areas of lithosphere. A superplume is thought to have uplifted a vast plateau region in southern Africa, for example.

Mantle plumes and hot spots are accepted by most geologists, but a minority are skeptical. Some think current ideas about mantle plumes and hot spots need major overhaul, while others deny that plumes and hot spots exist at all. They argue that the pressure deep in the mantle is far too great to allow mantle plumes to rise, and point out that there is little sign of the unusual heat deep in the mantle that should underly hot spots. If the bends in the Hawaiian-Emperor, Gilbert, and Tokelau chains formed when the Pacific Plate changed direction, as claimed by the hot spot hypothesis, they should all be the same age. The Hawaiian-Emporer and Gilbert bends are both estimated to be around 47 million years old, but the bend in the Tokelau chain is estimated at 57 million years. This and other evidence suggests that hot spots move from place to place, contrary to the long-held hypothesis that they remain stationary under the moving plates.

Mantle plume skeptics argue that the volcanic activity attributed to hot spots actually occurs because unusual stress or weakness in the lithospere causes a plate to crack, allowing magma to well up from the shallow—not deep—mantle. They explain island chains by rifts in the lithosphere that gradually extend like a crack in a windshield. They propose that Iceland formed not over a hot spot but at a weakened, ancient fault where North America and Europe collided 400 million years ago as part of the formation of Pangaea.

The debate over mantle plumes and hot spots shows no signs of abating, but both sides can explain an unusual feature of the Hawaiian Islands. About a quarter of the shallow-water fish species and one-fifth of shallow-water molluscs there are endemic, meaning they are found nowhere else. This is one of the highest rates of marine endemism anywhere, but even the oldest island, Kua'i, at only 5 million years old, is far too young for so many unique species to have evolved there. These species probably originated on much older islands in the chain. As the islands sank to become seamounts, the animals moved to shallow waters on newer islands that appeared nearby, whether because of a hot spot or a crack in the crust.

because the lithosphere has sunk into the mantle under the weight of the island, and also because sea level has risen. The abyssal plain and seamounts are home to a tremendous variety of marine life (see "Biodiversity in the Deep Sea," p. 375).

At trenches, where the plate descends into the mantle, the sea floor slopes steeply downward. Trenches are the deepest parts of the world ocean. The Mariana Trench in the western Pacific is the deepest place of all, at 11,022 m (36,163 ft) deep.

The Mid-Ocean Ridge and Hydrothermal Vents

The mid-ocean ridge itself is an environment that is unique in the ocean. As noted previously, the ridge is formed when material rising from the mantle pushes up the oceanic crust. Right at the center of the ridge, however, the plates are pulling apart. This leaves a great gap or depression known as the **central rift valley.** The floor and sides of the valley are riddled with crevices and fractures. Seawater seeps down through these cracks until it gets heated to very high temperatures by the hot mantle material (Fig. 2.25). The heated water then forces its way back up through the crust and emerges in **hydrothermal vents,** or deep-sea hot springs.

The water coming from many hydrothermal vents is warm, perhaps 10° to 20°C (50° to 68°F), much warmer than the surrounding water (see "The Three-Layered Ocean," p. 53). At some vents, however, the water is blisteringly hot, up to 350°C (660°F). The water is so hot that when scientists first tried to measure its temperature the thermometer they were using started to melt! To take accurate readings, they had to return with a specially designed thermometer.

As the hot water seeps through cracks in the earth's crust, it dissolves a variety of minerals, mainly **sulfides.** When the mineral-laden hot water emerges at the vent, it mixes with the surrounding cold water and rapidly cools. This causes many of the minerals to solidify, forming mineral deposits around the vents. **Black smokers** (Figs. 2.26 and 2.27) are one type of deposit found at hydrothermal vents. These are chimney-like structures that progressively build up around a vent as the minerals solidify. The "smoke" is actually a dense cloud of mineral particles.

When hydrothermal activity was first discovered it was thought to be confined to mid-ocean ridges. Hydrothermal vents, complete with black smokers and other mineral deposits, have since been found behind trenches. They result from the same volcanic activity that creates island arcs (see "Sea-Floor Spreading and Plate Tectonics," p. 27). Relatively cool (40° to 75°C, or 105° to 170°F) vents have also been discovered near, but not at, mid-ocean ridges. These vents produce chimneys of carbonate rather than sulfide minerals and are caused by chemical reactions between seawater and newly formed oceanic crust rather than by volcanic activity. One such chimney rises 60 m (200 ft) above the sea floor, making it the tallest hydrothermal vent known.

Deep-sea hot springs are of great interest not only to geologists, but also to biologists. The discovery of unexpectedly rich marine life around hydrothermal vents was one of the most exciting finds in the history of marine biology. These organisms are discussed in Chapter 16 (see "Hot Springs, Cold Seeps, and Dead Bodies," p. 374).

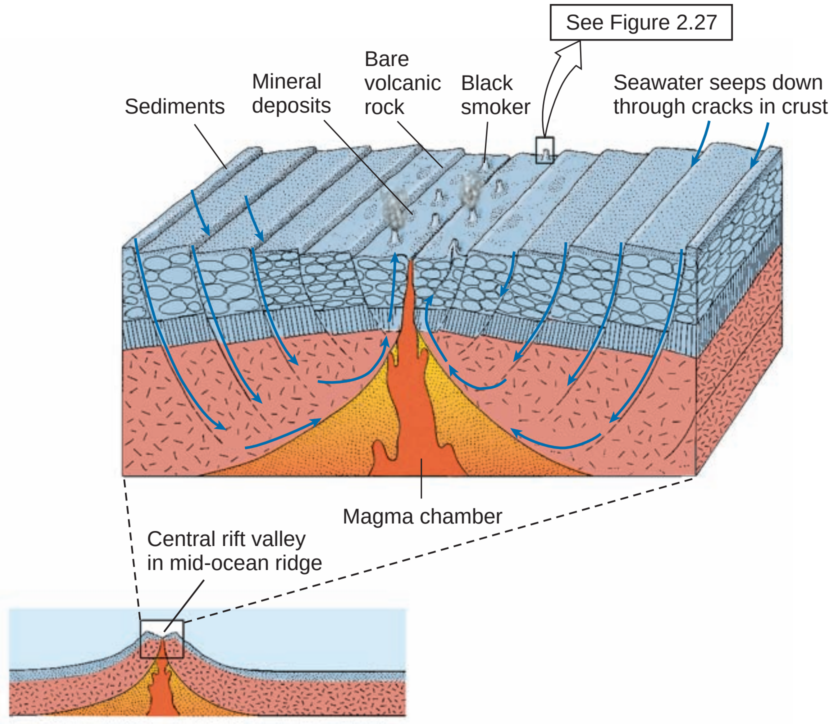
See Figure 2.27
Sediments
Mineral deposits
Bare volcanic rock
Black smoker
Seawater seeps down through cracks in crust
Magma chamber
Central rift valley in mid-ocean ridge

FIGURE 2.25 A cross section of a mid-ocean ridge showing how seawater seeps down through cracks in the crust, is heated, and reemerges in underwater hot springs.

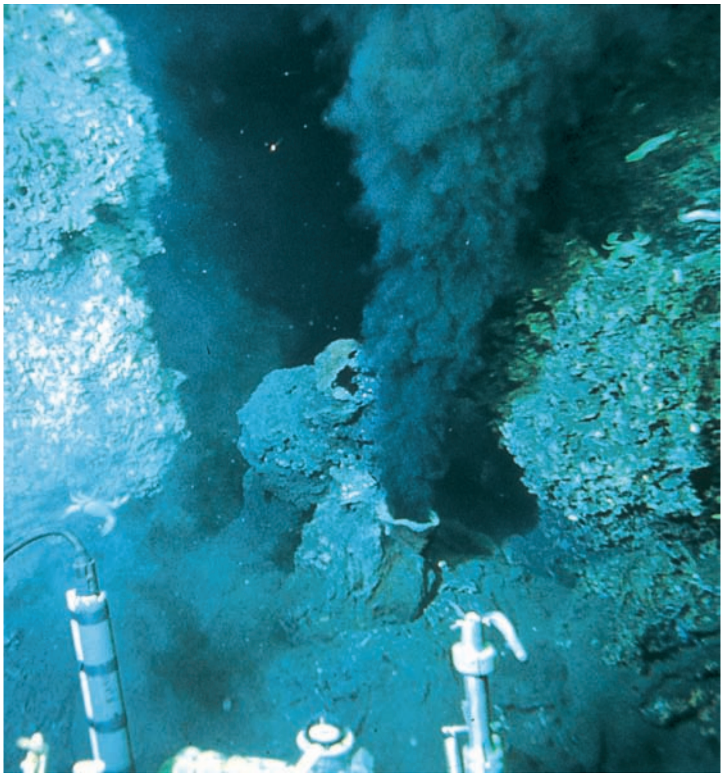

FIGURE 2.26 Black smokers are common in hydrothermal vent areas. The black "smoke," actually composed of mineral particles, rises because the water emerging from the black smoker is much warmer than the surrounding water. This photo was taken at the Galápagos vent, a part of the East Pacific Rise. The instruments in the foreground belong to *Alvin,* from which the photo was taken.

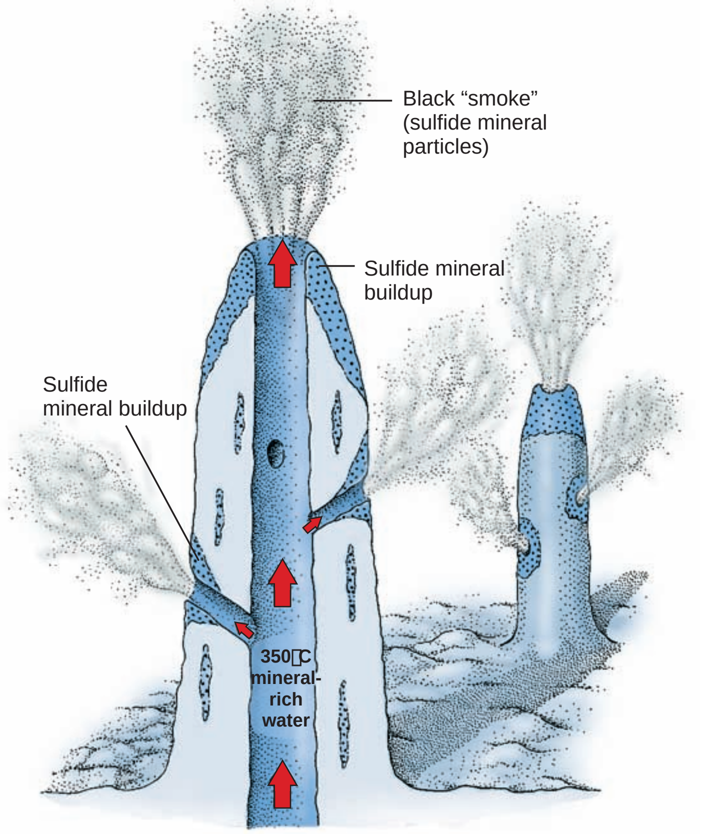
Black "smoke" (sulfide mineral particles)
Sulfide mineral buildup
Sulfide mineral buildup
350°C mineral-rich water

FIGURE 2.27 Cross section of a black smoker. Minerals are deposited as a precipitate when hot, mineral-laden water emerging from the rift zone meets the cold ocean water. Over time these mineral deposits build up the chimney of the black smoker.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Plate tectonics works today in the same way as in the past. Can you project the future positions of the continents by looking at a map of their present positions and the positions of the mid-ocean ridges (see Fig. 2.5)? Which oceans are growing and which are shrinking? Where will new oceans form?
2. Why are most oceanic trenches found in the Pacific Ocean?
3. Scientists who study forms of marine life that lived more than 200 million years ago usually obtain fossils not from the sea floor, but from areas that were once undersea and have been uplifted onto the continents. Why?
4. What are some of the major pieces of evidence for the theory of plate tectonics? How does the theory explain these observations?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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3

CHAPTER

Chemical and Physical Features of Seawater and the World Ocean

A flock of Antarctic prions (*Pachyptila desolata*) flies above the spray of waves crashing onto an iceberg.

"Everybody talks about the weather, but nobody does anything about it." Often attributed to Mark Twain, this quote by Twain's collaborator, Charles Dudley Warner, expresses the plight of marine organisms as well as people. From the point of view of marine organisms, crashing waves and icy waters are just part of the ocean's "weather," as are wind, tides, currents, salt, and other chemical and physical features of the ocean.

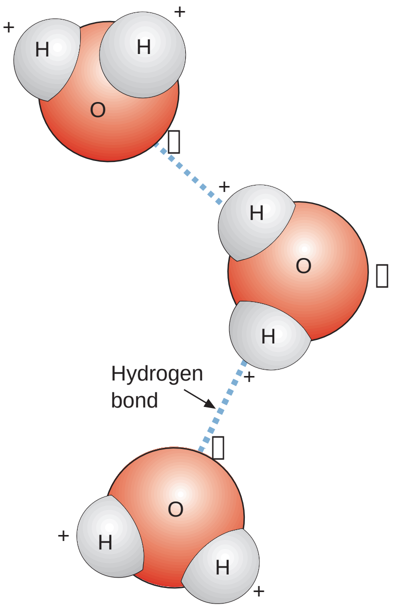
Because marine organisms can't control the physical and chemical nature of their environment, they simply have to "grin and bear it"—that is, they have to *adapt* to the place where they live, or live somewhere else. Which organisms occur at a given place in the ocean and the way they live are largely controlled by chemical and physical factors. To understand the biology of marine organisms, therefore, we must know something about the environment in which they live. Chapter 3 describes the chemistry and physics of the oceans in relation to life in the sea.

THE WATERS OF THE OCEAN

We often think of water as commonplace because there is so much of it around. From a cosmic perspective, though, water is not common at all. Earth is the only known planet with liquid water on its surface.

Even so, most of us never give water a second thought, unless we happen to be hot or thirsty. Water quenches our thirst

FIGURE 3.1 The different ends of water molecules have opposite electrical charges. The oxygen (O) end has a weak negative charge, the hydrogen (H) end a slight positive charge. Opposite charges attract each other like the opposite poles of a magnet, so the oxygen end of one molecule is attracted to the hydrogen end of neighboring molecules. These weak attractions between water molecules are known as hydrogen bonds.



because it makes up most of our bodies. Marine organisms, too, are mostly water—80% or more by weight in most cases, and in jellyfishes over 95%. Water not only fills the ocean, it makes possible life itself.

The Unique Nature of Pure Water

All matter is made of **atoms.** Only 118 or so known substances (physicists argue about the exact number) are composed of a single kind of atom; these are called **elements.** In all other substances two or more atoms are chemically combined into larger particles called **molecules.** Water molecules are made up of one oxygen atom, which is relatively large, and two small hydrogen atoms. The oxygen and hydrogen atoms have weak, opposite charges that create electrical attractions, or **hydrogen bonds,** between adjacent water molecules (Fig. 3.1). Hydrogen bonds are much weaker than the covalent bonds that hold the water molecule together, but they make water different from any other substance on earth.

The Three States of Water Any substance can exist in three different states, or phases: solid, liquid, or gas. Water is the only substance that naturally occurs in all three states on earth.

In liquid water, hydrogen bonds hold most of the molecules together in small groups (Fig. 3.2). The molecules are in constant motion, however, and because the hydrogen bonds are weak the groups constantly break apart and re-form. Temperature reflects the average speed of the molecules—the faster they move, the higher the temperature. When a molecule moves fast enough it breaks free of all the hydrogen bonds and escapes from the liquid phase into the gaseous or vapor phase. This is the process of **evaporation.**

In water vapor the molecules are not held together by hydrogen bonds. They are separate and much farther apart than in the liquid (Fig. 3.2). As temperature rises so does the evaporation rate, since the molecules move faster and more escape the hydrogen bonds. When the water gets hot enough, nearly all the bonds are broken and many molecules enter the vapor state at once; in other words, the water boils.

When liquid water cools, the molecules not only move slower, they pack closer together and take up less space, so that the volume of water decreases. Because the volume decreases without changing the mass, the water gets **denser.** As seawater gets colder, therefore, it gets more dense. As we shall see, cold seawater tends to sink in the ocean. Fresh water also gets denser as it gets colder, but only down to a temperature of about 4°C (39°F). Below 4°C fresh water gets less dense as it cools.

Water freezes when the molecules move so slowly that the hydrogen bonds take over, locking the molecules into a fixed, three-dimensional pattern known as a **crystal.** In ice crystals the molecules are further apart than in liquid water, so water expands

Density The mass of a given volume of a substance.

$$\textbf{density} = \frac{\textbf{mass}}{\textbf{volume}}$$

- Chapter 2, p. 21

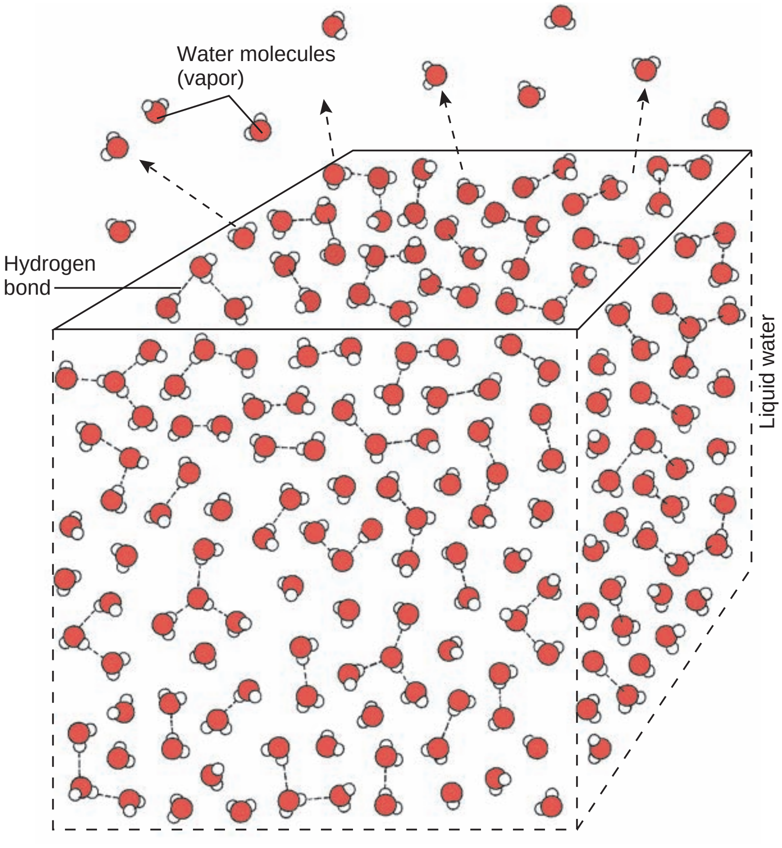


FIGURE 3.2 The molecules in liquid water form groups of various sizes held together by hydrogen bonds. The molecules are moving too rapidly to be held permanently in place, so the groups constantly break up and re-form. Evaporation occurs when molecules break free of hydrogen bonds and enter the gaseous state. Molecules of water vapor are much farther apart than in the liquid state and are not held in groups by hydrogen bonds.

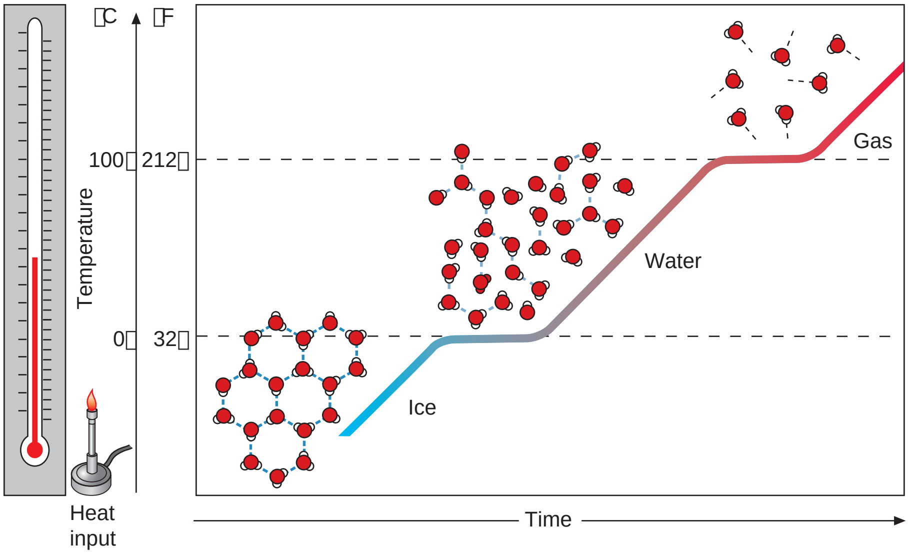


FIGURE 3.3 The molecular structure of water changes with temperature. In ice, hydrogen bonds hold the vibrating molecules in a hexagonal pattern. As heat is added, the ice warms up and the molecules vibrate more rapidly until they break free of the crystal structure. When this happens, the ice melts. While the ice is melting, added heat is absorbed by breaking hydrogen bonds, not by increasing the temperature. When the ice is completely melted, additional heat causes the temperature to rise again. Some molecules gain enough speed to break free of all the bonds and evaporate. At 100°C (212°F) nearly all the hydrogen bonds are broken and the water boils.

as it freezes. Because the same mass of water occupies more volume as ice than as liquid water, ice is less dense and floats. Water is extremely unusual in being less dense as a solid than a liquid, a property that is very important for aquatic organisms, both freshwater and marine. A layer of floating ice leaves plenty of water below where organisms can live, and insulates the water below so that it doesn't freeze. If ice were denser than liquid water, the ocean would freeze from the bottom and be much less hospitable to life.

Seawater becomes denser as it cools, until it freezes. Ice is less dense than liquid water.

Heat and Water In ice, vibrating water molecules are held in place in the ice crystal by hydrogen bonds. The bonds must be broken before the molecules can begin to move around, which is what happens when ice melts (Fig. 3.3). Because of this, ice melts—or, moving in the opposite direction, freezes—at a much higher temperature than similar substances that do not form hydrogen bonds. If not for the hydrogen bonds, ice would melt at about −90°C (−130°F) instead of 0°C (32°F)!

Not only does ice melt at a comparatively high temperature, it absorbs a lot of heat when it melts. The amount of heat required to melt a substance is called its **latent heat of melting.** Water has a higher latent heat of melting than any other commonly occurring substance. The reverse is also true: A great deal of heat must be removed from liquid water to freeze it. It thus takes a long period of very cold weather before a body of water will freeze.

In melting ice, added heat breaks more hydrogen bonds rather than increasing the speed of molecular motion, so the temperature of the ice-water mixture remains at a constant 0°C (32°F) until all the ice melts. That is why ice keeps drinks cold: Added heat goes into melting the ice, not raising the temperature.

Once all the ice has melted, added heat again makes the molecules move faster and so raises the water temperature. Some of the heat energy, however, still goes into breaking hydrogen bonds rather than increasing the speed of molecular motion. It therefore takes a lot of heat to raise the temperature. The amount of heat needed to raise a substance's temperature by a given amount, or its **heat capacity,** reflects how much heat the substance can store. Water has one of the highest heat capacities of any naturally occurring substance. Water's ability to absorb a lot of heat with a relatively small increase in temperature is why it is used as a coolant, in car engines for example. More importantly for marine organisms, water's high heat capacity means that most of them are not subjected to the rapid and sometimes drastic temperature changes that occur on land (Fig. 3.4).

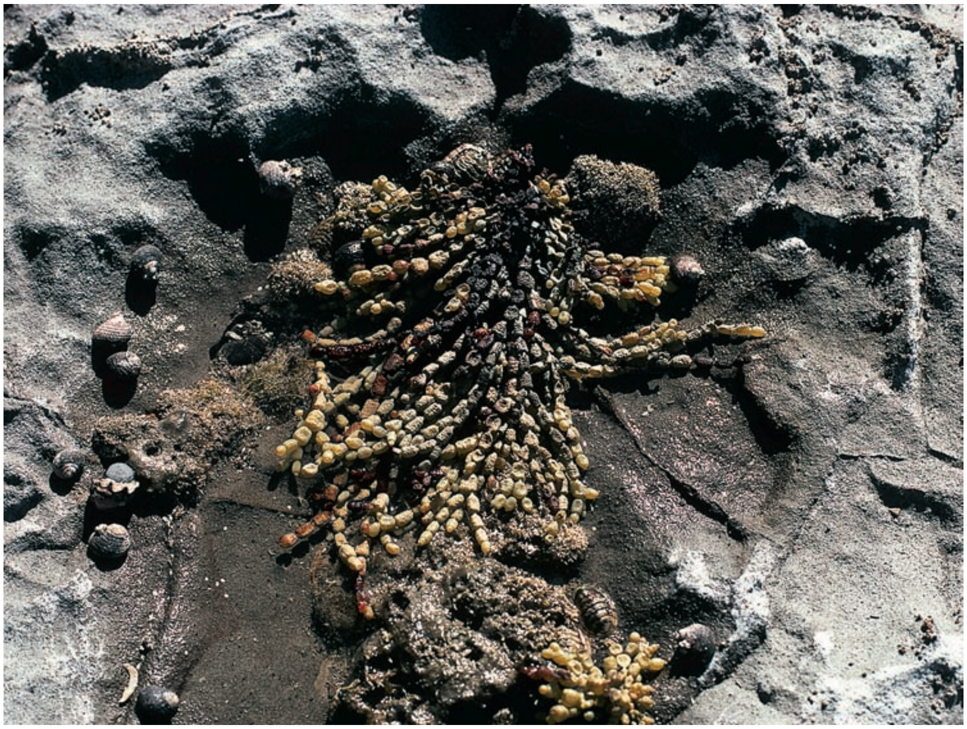


FIGURE 3.4 In the heat of the sun, this seaweed (*Hormosira banksii*) in New Zealand is beginning to shrivel. Shore organisms that are exposed to the air during low tide are subjected to much more extreme temperatures than organisms that are always submerged.

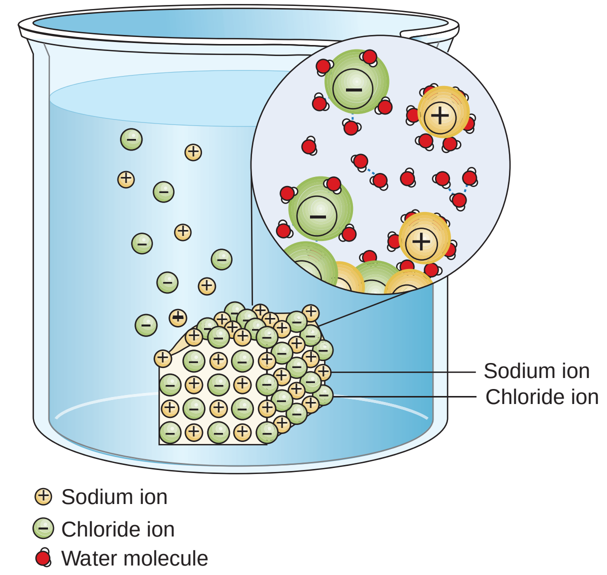


FIGURE 3.5 Within a crystal of table salt, or sodium chloride, the ions are held together by the attractions between opposite charges. Because the charges on the ions are much stronger than the charges on a water molecule, the bonds between ions are stronger than hydrogen bonds. When the salt is placed in water, the slightly charged water molecules are attracted to the charges on the ions. The water molecules cluster around the ions. This weakens the bonds between ions, which separate, or dissociate.

Water also absorbs a great deal of heat when it evaporates; that is, it has a high **latent heat of evaporation.** Again this is due to hydrogen bonds: Only the fastest-moving molecules, those with the most energy, can break the bonds to enter the gaseous phase. Because the fastest molecules leave the liquid phase, those left behind have a lower average velocity and therefore a lower temperature. This is known as **evaporative cooling,** which our bodies utilize when evaporating perspiration cools our skin.

Water has the highest latent heats of melting and evaporation and one of the highest heat capacities of any natural substance.

Water as a Solvent Water can dissolve more things than any other natural substance and is often called the universal solvent. Water is especially good at dissolving **salts.** Salts are made up of particles with opposite electrical charges. Such electrically charged particles, which can be either single atoms or groups of atoms, are known as **ions.** For example, ordinary table salt, or sodium chloride (NaCl), consists of a positively charged sodium ion (Na^+) combined with a negatively charged chloride ion (Cl^-). The oppositely charged ions are joined by the same electrical attraction that creates hydrogen bonds between water molecules. Ions have much stronger electrical charges than the opposite ends of the water molecule, however, so these ionic bonds are much stronger than hydrogen bonds. If no water is present, the ions bind strongly together to form salt crystals (Fig. 3.5).

When a salt crystal is placed in water, the strongly charged ions attract the water molecules—with their weak charges—like iron filings to a magnet. A layer of water molecules surrounds each ion, insulating it from the surrounding ions (Fig. 3.5). This greatly weakens the ionic bonds that hold the salt crystal together. The ions pull apart, or **dissociate,** and the salt dissolves.

Seawater

The characteristics of seawater are due both to the nature of pure water and to the materials dissolved in it. Some of the solids dissolved in seawater are produced by the chemical **weathering** of rocks on land and are carried to the sea by rivers (Fig. 3.6). Other materials come from the earth's interior. Most

Weathering The physical or chemical breakdown of rocks.
- Chapter 2, p. 32

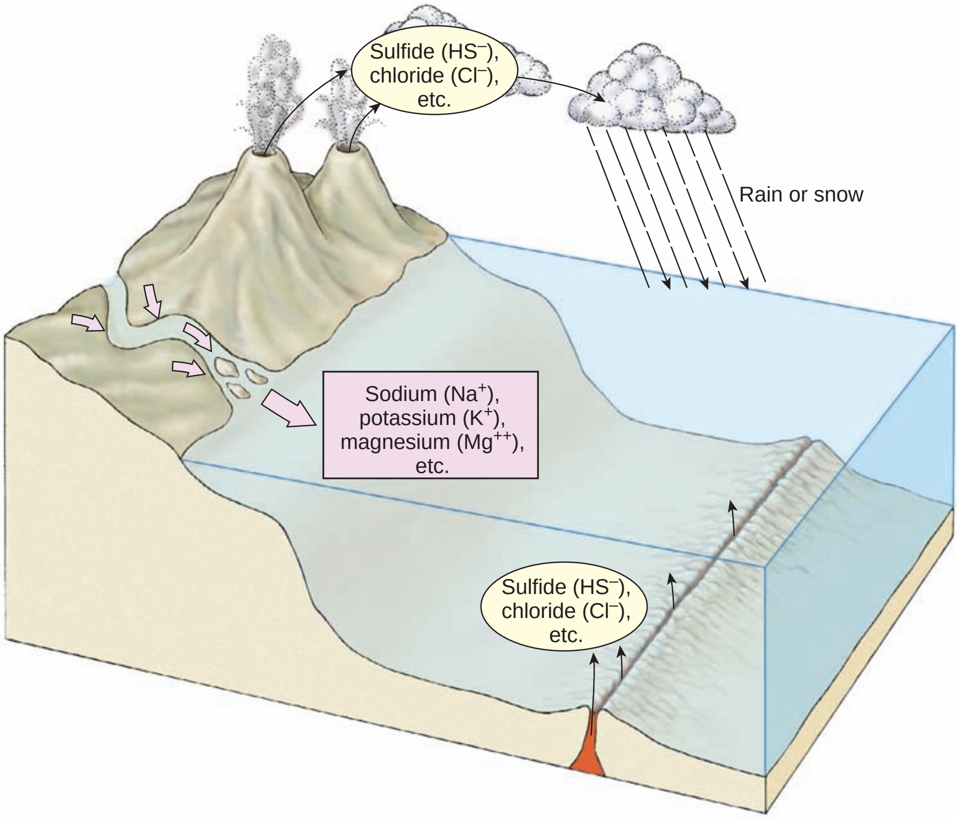

Sulfide (HS^-), chloride (Cl^-), etc.
Rain or snow
Sodium (Na^+), potassium (K^+), magnesium (Mg^{++}), etc.
Sulfide (HS^-), chloride (Cl^-), etc.

FIGURE 3.6 Not all ions in seawater enter the ocean at the same place. Positive ions like sodium and magnesium come mostly from the weathering of rocks and are carried to the sea by rivers. Negative ions like chloride and sulfide enter the ocean at hydrothermal vents and from volcanoes via precipitation. If the ocean was not thoroughly mixed, coastal water would have a relatively high proportion of sodium and magnesium. Deeper water, influenced by hydrothermal input, would be rich in chloride and sulfate, which is produced from sulfide. Actually, the proportions of ions do vary right near river mouths and hydrothermal vents, but most of the ocean is well mixed and the rule of constant proportions holds.

of these are released into the ocean at **hydrothermal vents.** Some are released into the atmosphere from volcanoes and enter the ocean in rain and snow.

Salt Composition Seawater contains at least a little of almost everything, but most of the **solutes,** or dissolved materials, are made up of a surprisingly small group of ions. In fact, only six ions compose over 99% of the solids dissolved in seawater (Table 3.1). Sodium and chloride account for about 85%, which is why seawater tastes like table salt.

When seawater evaporates, the ions in it are left behind and combine to form various salts. **Salinity** is defined as the total amount of salt dissolved in seawater. Salinity is usually expressed as the number of grams of salt left behind when 1,000 grams of seawater are evaporated. If 35 grams of salt are left from evaporating 1,000 grams of seawater, for example, the seawater had a salinity of 35 parts per thousand, or 35‰.

Today salinity is rarely measured by evaporating water samples; electronic instruments are used instead. Because of their electrical charges, ions are good electrical conductors. The conductivity of seawater therefore reflects the concentration of dissolved ions, that is, the salinity. Oceanographers often express salinity determined from conductivity measurements in **practical salinity units (psu)** rather than parts per thousand, but the two units are numerically the same: 35 psu is equivalent to 35‰.

The salinity of water greatly affects the organisms that live in it. Most marine organisms die in fresh water. Even slight changes in salinity harm some organisms. Many, especially those that live in river mouths or other places where the salinity is prone to fluctuations, have evolved specific mechanisms to cope with salinity changes (see "Regulation of Salt and Water Balance," p. 74).

Table 3.1

The Composition of Seawater of 35‰ Salinity

Although the concentration varies slightly from place to place in the ocean, the percentage of total salinity of each ion remains constant.

Ion	Concentration ‰	Percentage of Total Salinity
Chloride (Cl^-)	19.345	55.03
Sodium (Na^+)	10.752	30.59
Sulfate (SO_4^{-2})	2.701	7.68
Magnesium (Mg^{+2})	1.295	3.68
Calcium (Ca^{+2})	0.416	1.18
Potassium (K^+)	0.390	1.11
Bicarbonate (HCO_3^-)	0.145	0.41
Bromide (Br^-)	0.066	0.19
Borate ($H_2BO_3^-$)	0.027	0.08
Strontium (Sr^{+2})	0.013	0.04
Fluoride (F^-)	0.001	0.003
Other dissolved material	<0.001	<0.001

Organisms are affected not only by the total amount of salt, but also by the kind of salt. The composition of seawater can be determined by analyzing the salts left after evaporation. In fact, that is how the information in Table 3.1 was obtained.

The chemist William Dittmar analyzed seawater samples from the *Challenger* expedition and found that the percentage of the major ions in seawater remained constant even though the total amount of salt varied slightly from place to place. Chloride ion, for example, nearly always makes up 55.03% of however much salt is present. This principle is called the **rule of constant proportions.**

The rule of constant proportions states that the relative amounts of the various ions in seawater are always the same.

The proportions of different ions do in fact vary slightly, especially in coastal areas where rivers bring in large amounts of positively charged ions or near hydrothermal vents (Fig. 3.6). In some places intense biological activity also affects ion ratios. Still, in most of the oceans the proportions remain remarkably constant. This indicates that for the most part the oceans are chemically well mixed, and that ocean salinity varies almost entirely as a result of the addition or removal of pure water rather than the addition or removal of salts. If salinity varied by adding or removing any particular salt, then the relative amounts of the ions in the seawater would change. If magnesium chloride ($MgCl_2$) were added, for example, then the proportions of magnesium and chloride would go up. Thus, although marine organisms are exposed to changes in total salinity, they rarely have to deal with changes in the ratios of the various ions. This makes it easier for them to control their internal salt and water balance.

Water is removed from the ocean primarily by evaporation, and to a lesser extent by freezing. When seawater freezes, the ions are excluded from the forming ice. They are left behind in the unfrozen water, increasing its salinity, and the ice is almost pure water. That is why icebergs are not salty. Water is added by **precipitation**—rain and snow—and, to a lesser extent on short timescales, by the melting of glaciers and polar ice.

The average salinity of the ocean is about 35‰. The open ocean varies relatively little, between about 33‰ and 37‰, depending mostly on the balance between evaporation and precipitation. Partially enclosed seas may have more extreme salinities. The Red Sea, for instance, is in a hot, dry region where evaporation predominates over precipitation, so it is very salty, about 40‰. Near coasts or in enclosed basins, runoff from rivers may have a strong effect. River runoff gives the Baltic Sea a typical salinity at the surface of only about 7‰, for example.

The "other dissolved material" listed in Table 3.1 includes substances such as essential nutrients that, though present in tiny amounts, are critically important to marine life. Compounds containing nitrogen (N), phosphorus (P), and iron (Fe) are particularly important and their availability determines the biological productivity of much of the oceans (see "The Importance of Nutrients," p. 68, and "Nutrients," p. 346).

FIGURE 3.7 Niskin bottles are one of several types of water sampling bottles. The bottles are clamped to a cable and lowered to the desired depth with both ends open. A weight called a messenger is sent down from the surface. The spring-loaded end caps then snap shut, trapping a sample of seawater in the bottle.

Salinity, Temperature, and Density We have already seen that temperature greatly affects water's density. Salinity also influences seawater density: The saltier the water, the denser it is. The density of seawater therefore depends on both its temperature and its salinity.

> The temperature and salinity of seawater determine its density: It gets denser as it gets saltier, colder, or both.

Temperature in the open ocean varies between about −2° and +30°C (28° and 86°F). Temperatures below 0°C (32°F) are possible because salt water freezes at a colder temperature than pure water. This is one reason that the ocean is less prone to freezing than lakes and rivers.

Temperature in the ocean varies considerably more than salinity, so as a practical matter density is usually controlled more by temperature than salinity. Exceptions do occur, however, and both the temperature and salinity of ocean water still need to be measured to determine the density.

Temperature and salinity can be measured by lowering specially designed bottles and thermometers on a wire to the desired depth (Fig. 3.7). Then a weight called a messenger is released to slide down the wire, triggering the bottles to snap shut and trap a water sample that can be analyzed for salinity. The thermometers are also triggered to "freeze" the temperature reading so that it doesn't change as the thermometer is retrieved.

A series of bottles can be attached to the cable to measure temperature and salinity, and therefore density, at several depths at once (Fig. 3.8). A graph that shows the temperature at different depths in the ocean is called a temperature **profile.** A temperature profile obtained from a given location can be thought of as showing the temperature in a vertical shaft of water, or **water column,** extending down from the surface. Profiles can also be plotted for salinity, density, or any other characteristic. In a profile the vertical axis appears "upside down," as shown in Figure 3.8.

> A profile is a plot that shows temperature, salinity, or any other characteristic of seawater at various depths in the water column.

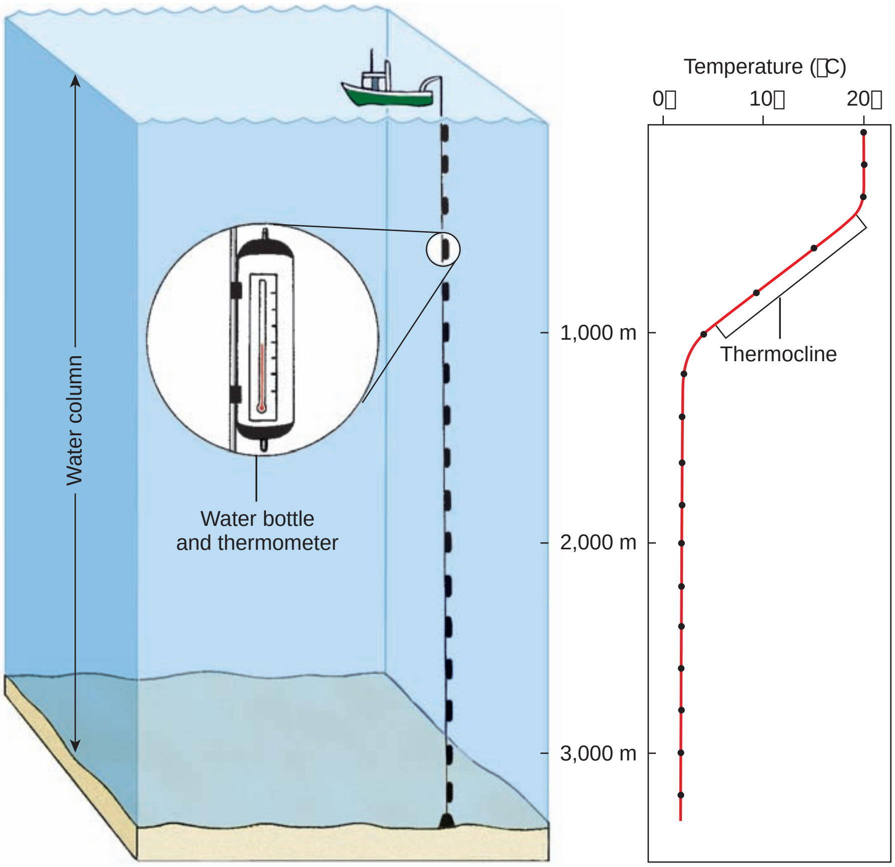
Using bottles and thermometers is time-consuming and expensive. Today oceanographers usually use electronic sensors to quickly and accurately record salinity, temperature, and depth

Hydrothermal Vents Undersea hot springs associated with mid-ocean ridges.

- Chapter 2, p. 37

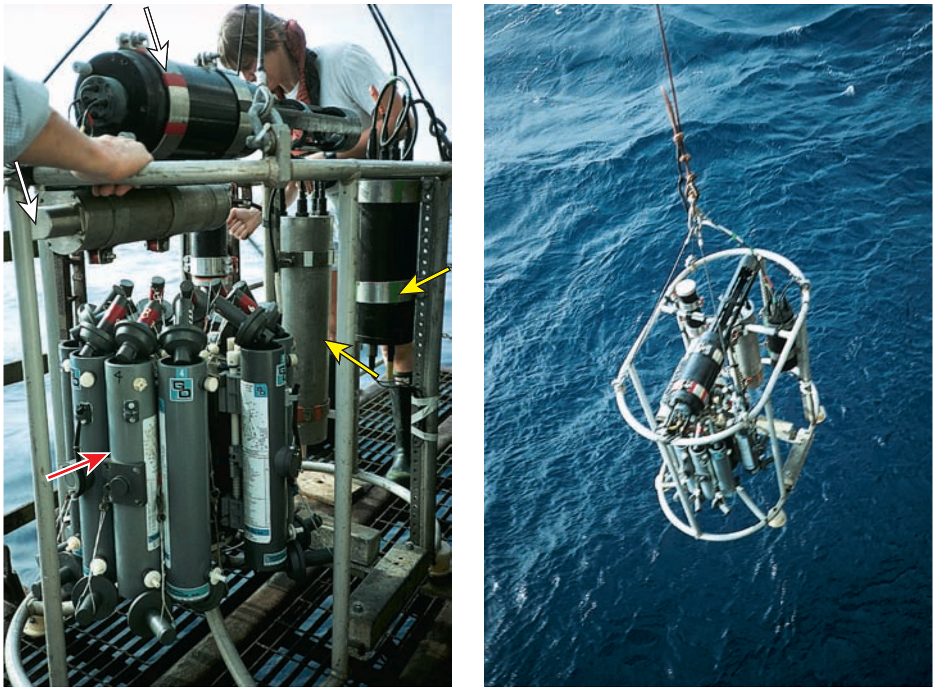
The *Challenger* expedition (1872–1876) marked the birth of modern oceanography.

- Chapter 1, p. 3



(a) (b)

FIGURE 3.8 (*a*) Sampling bottles can be used to measure temperature and salinity at several depths at once. (*b*) The results are plotted on a profile, or a graph showing how temperature, salinity, or any other property varies with depth. This example shows a temperature profile. Temperature is measured only where the bottles are (dots) and the temperature between the bottles (red line) must be inferred. The zone in which the temperature rapidly drops as it gets deeper is called a thermocline.



(a) (b)

FIGURE 3.9 (*a*) Instead of being hung on a wire individually, water sampling bottles (red arrow) are now usually mounted in a "rosette" to a single frame. A variety of electronic instruments (yellow arrows) that measure temperature, salinity, light, water clarity, and other factors can also be mounted on the frame, (*b*) which is then lowered through the water column. Many of the instruments provide real-time information to computers on the surface.

throughout the water column, rather than just at certain depths. **CTDs** (*c*onductivity-*t*emperature-*d*epth meters) are widely used in conjunction with other instruments (Fig. 3.9). Expendable bathythermographs (XBTs), which measure temperature but not salinity profiles, are even disposable.

Though temperature, salinity, and various other things can be measured electronically, many other measurements still require a water sample, so Niskin bottles and similar devices remain in use. These days, oceanographers usually mount all the open bottles on a single rack (Fig. 3.9) rather than stringing them along the wire. To collect samples from different depths, each bottle is closed at a different time while the rack is lowered. The rack is easier to use than a series of individual bottles.

Even with electronic instruments, measurements from ships can be made in only one place at a time. To study a large area, the ship has to steam from place to place. In the meantime, conditions might change because of currents or the weather. One alternative is to use a number of ships at once. This is expensive, however, and is not done often. Today oceanographers increasingly make their measurements with automated instruments (see "Ocean Observing Systems," p. 10).

Another way to get the big picture is to use satellites. Satellites can measure conditions only near the surface, but they give instantaneous coverage of a large area (Fig. 3.10). Furthermore, a series of measurements can be made in a short

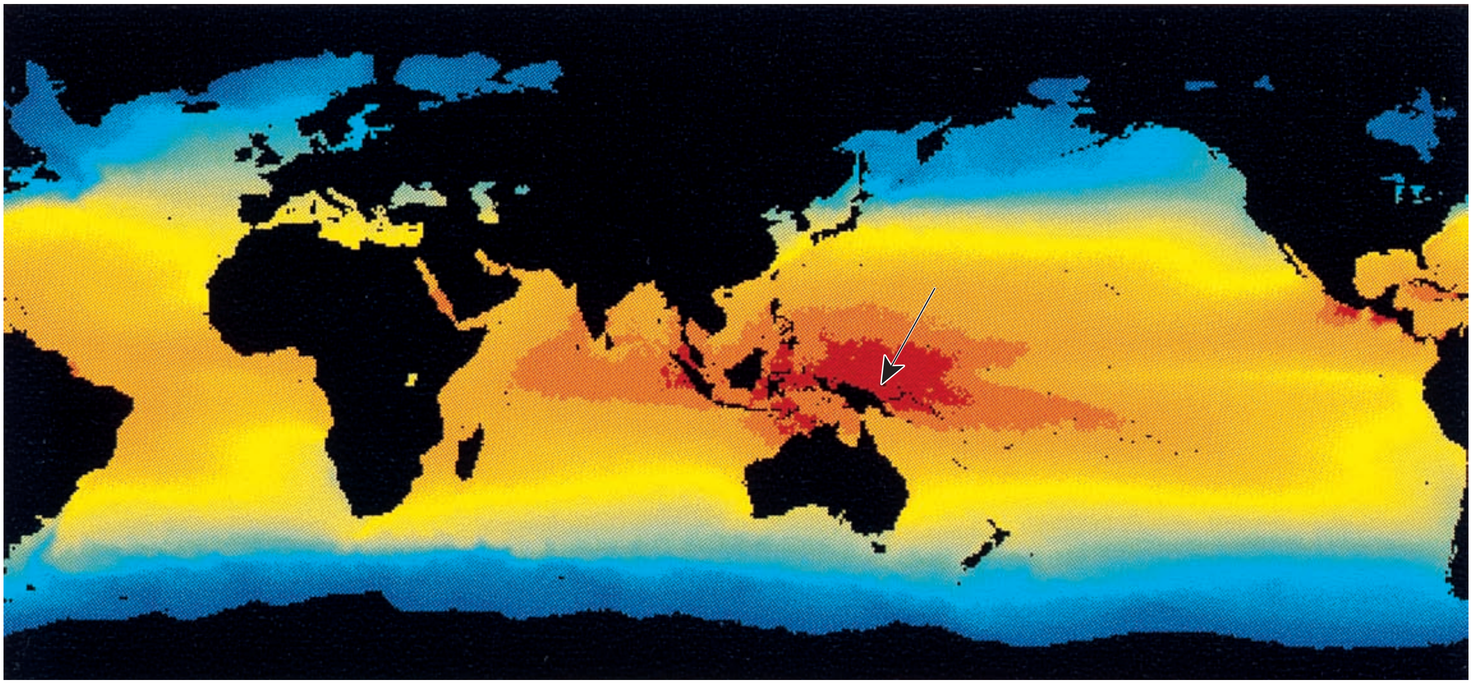


FIGURE 3.10 This satellite image shows the temperature of the ocean surface. The coldest water is shown in blue, the warmest in red. The large patch of very warm (29.5°C, 85.1°F) water just north of the island of New Guinea (arrow) contains the ocean's largest reservoir of heat and strongly influences the climate of the entire planet. During El Niño years, for example, the pool of warm water moves east to the central Pacific (see "The El Niño–Southern Oscillation Phenomenon," p. 353).

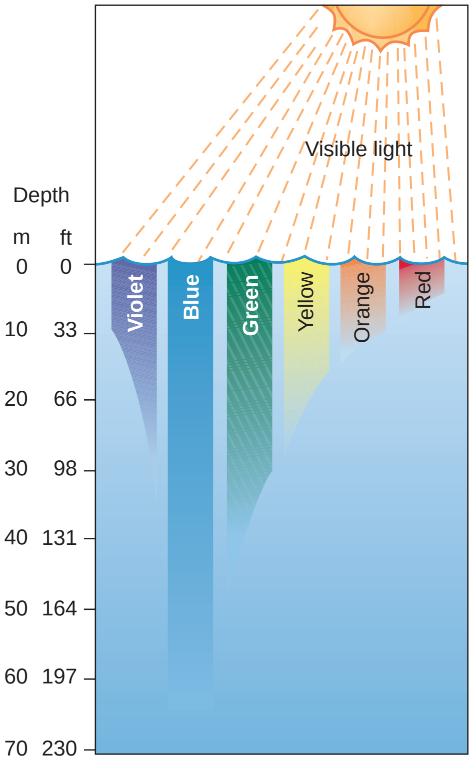


FIGURE 3.11 Different colors of light penetrate to different depths in the ocean. In clear ocean water blue light penetrates the deepest, red light the least. Coastal waters often contain materials that absorb blue light so that green penetrates deepest.

time. This makes it possible to follow rapid changes in surface conditions that result from currents and weather.

Dissolved Gases There are gases as well as solid materials dissolved in seawater. For organisms the most important gases in the ocean are **oxygen (O_2), carbon dioxide (CO_2),** and **nitrogen (N_2).** All three are found in the atmosphere and dissolve in seawater at the sea surface. Sometimes the reverse occurs and the sea surface releases gases to the atmosphere. This process is known as **gas exchange** between the ocean and atmosphere.

Unlike solids, gases dissolve better in cold than in warm water, so dissolved gas concentrations are higher in polar waters than in the tropics. Oxygen gas is not very soluble. The ocean contains between 0 and 8 milliliters of dissolved oxygen per liter of seawater, but more typically about 4 to 6 ml/l. A liter of air, by comparison, contains about 210 milliliters of oxygen, or 21% of the total volume. The amount of oxygen in the water is also strongly affected by organisms through **photosynthesis** and **respiration.** Much of the oxygen produced by photosynthesis in the ocean is released to the atmosphere. The relatively low dissolved oxygen level in seawater makes it more susceptible than air to oxygen depletion by respiration (see "The Oxygen Minimum Layer," p. 367).

Carbon dioxide is much more soluble than oxygen because it reacts chemically when it dissolves. As a result, CO_2 makes up more than 80% of the dissolved gas in the ocean, compared to less than 0.04% of air, and the ocean stores more than 50 times as much total CO_2 as the atmosphere. This makes the ocean critical to understanding the effects of human activities on the earth's climate (see "Special Report: Our Changing Planet," p. 231).

Transparency One of the most biologically important properties of seawater is that it is relatively transparent, so sunlight can penetrate into the ocean. This is vital because all photosynthetic organisms need light to grow. If seawater were not transparent, there would be very little photosynthesis in the sea, and then only right at the surface.

Sunlight contains all the colors of the rainbow, but not all colors penetrate seawater equally well. Clear ocean water is most transparent to blue light. Other colors are absorbed more than blue, so as depth increases more and more of these other colors are filtered out and soon only blue light remains (Fig. 3.11). Things that appear red on the surface look gray or black at depth because there is no red light to reflect off them and be seen (Fig. 3.12). At greater depths—about 1,000 m (3,300 ft) in the clearest water—even the blue light gets absorbed and only darkness remains.

Photosynthesis
$CO_2 + H_2O + \text{Sun energy} \rightarrow \underset{\text{(glucose)}}{\text{organic matter}} + O_2$

- Chapter 4, p. 66

Respiration
$\underset{\text{(glucose)}}{\text{organic matter}} + O_2 \rightarrow CO_2 + H_2O + \text{energy}$

- Chapter 4, p. 67

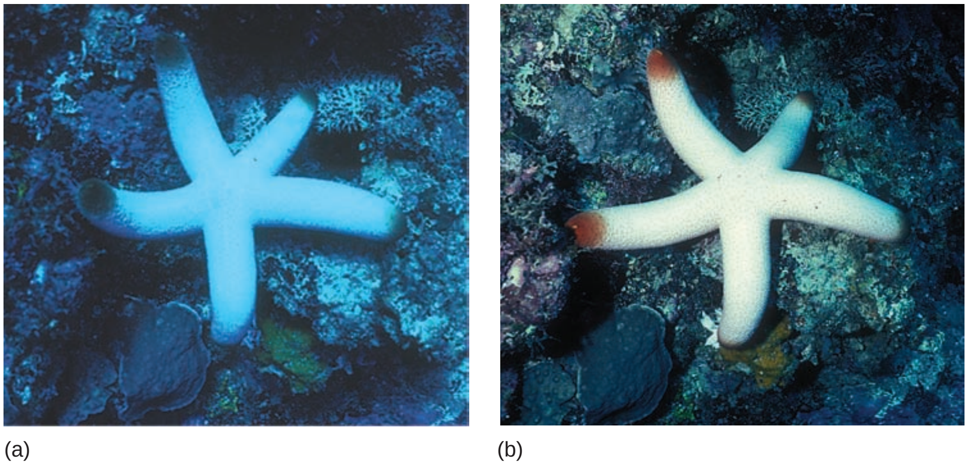

(a) (b)

FIGURE 3.12 At a depth of 30 m (98 ft) only blue light remains, and under natural lighting (*a*) this sea star (*Thromidia catalai*) appears light blue, with the tips of the arms almost black. (*b*) An electronic flash reveals the sea star's true colors.

The transparency of water is strongly affected by material that is suspended and dissolved in the water (Fig. 3.13). Obviously, muddy water is not as clear as clean water. Large quantities of plankton also reduce water transparency. Water near coasts often contains a lot of material brought in by rivers that gives coastal waters a greenish tint and makes them less transparent than the deep blue waters of the open ocean.

Pressure **Pressure** is another factor that changes dramatically with depth in the ocean. Organisms on land are under 1 **atmosphere** (14.7 pounds per square inch, or psi) of pressure at sea level—the weight of all the air above them. Marine organisms, however, are under the weight of water as well as the atmosphere. Since water is much heavier than air, marine organisms are under much more pressure than those on land. The pressure increases dramatically with depth because the amount of water above gets greater (Fig. 3.14). With each 10 m (33 ft) of increased depth, another atmosphere of pressure is added.

As the pressure increases, gases are compressed. Gas-filled structures inside organisms like air bladders, floats, and lungs shrink or collapse. This limits the depth range of many marine organisms. It also means that submarines and housings for scientific instruments must be specially engineered to withstand pressure. This greatly increases the difficulty, expense, and sometimes the danger of studying the sea. The reverse effect also causes problems: Organisms that contain gas-filled structures may be injured when brought up from the deep (Fig. 3.15).

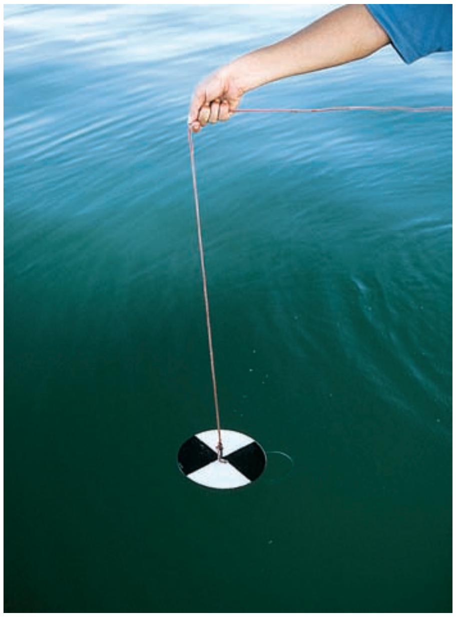


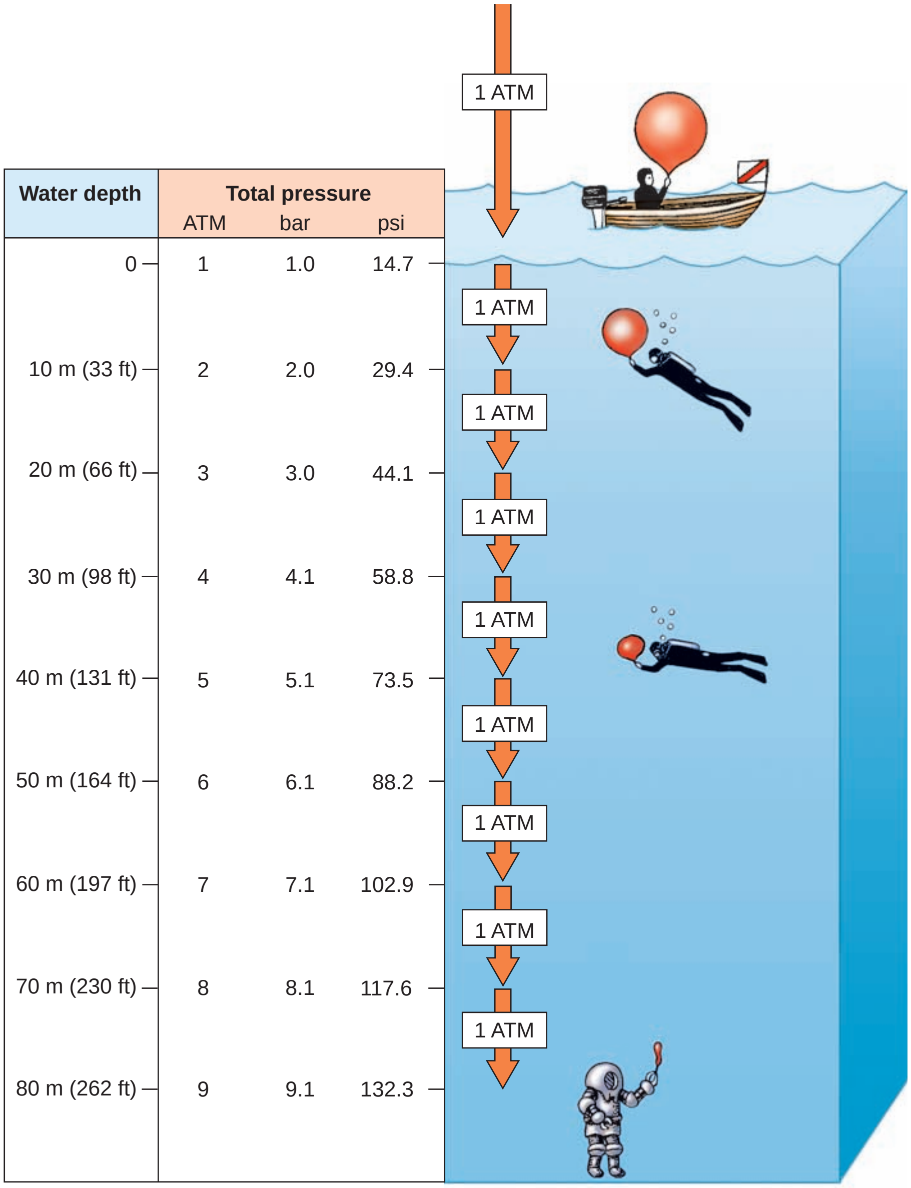
FIGURE 3.13 Sophisticated electronic instruments like those mounted to the frame in Figure 3.9 allow precise measurements of water clarity and light penetration. For surface waters, however, this simple instrument called a Secchi disk gives a surprisingly useful measurement of water clarity. The disk is slowly lowered to where it just ceases to be visible. The greater this depth, the clearer the water.

OCEAN CIRCULATION

The ocean never rests. Throughout its depths, currents move and mix ocean waters and transport heat, nutrients, pollutants, and organisms. Ocean circulation profoundly affects not only marine organisms and their habitats, but also the earth's climate and therefore all habitats on land.

Surface Circulation

The wind drives the strongest ocean currents, which occur in the surface layer. Both wind and surface currents are ultimately driven



Water depth	Total pressure		
	ATM	bar	psi
0	1	1.0	14.7
10 m (33 ft)	2	2.0	29.4
20 m (66 ft)	3	3.0	44.1
30 m (98 ft)	4	4.1	58.8
40 m (131 ft)	5	5.1	73.5
50 m (164 ft)	6	6.1	88.2
60 m (197 ft)	7	7.1	102.9
70 m (230 ft)	8	8.1	117.6
80 m (262 ft)	9	9.1	132.3

FIGURE 3.14 The pressure at any place depends on the weight pressing down from above. At the sea surface or on land, only the atmosphere is above. Divers and marine organisms, however, are also under the weight of the water column. The deeper the diver goes, the more water presses down from above and the greater the pressure. As the pressure increases, flexible gas-filled structures like the red balloon are compressed. Pressure can be measured in atmospheres (ATM), bars, pounds per square inch (psi) or other units.

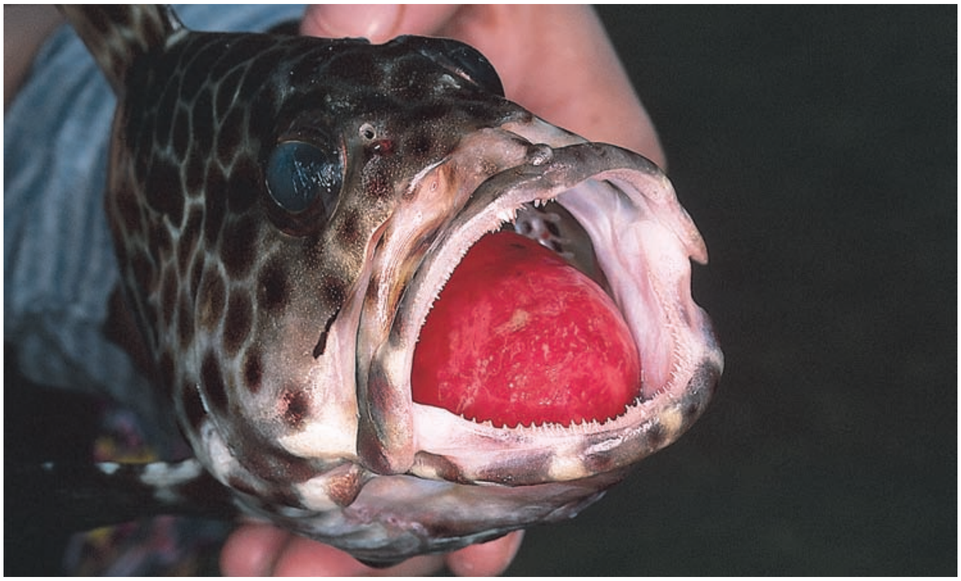


FIGURE 3.15 Many fishes, like this longfin grouper (*Epinephalus quoyanus*), have an internal air sac called a swim bladder. If the fish is brought to the surface too quickly, the bladder blows up like a balloon because of the decreased pressure. This fish's swim bladder has expanded so much that it has pushed its stomach out of its mouth. Fish like this sometimes survive if the bladder is carefully punctured and the fish returned to the water, though there are often severe internal injuries.

by heat energy from the sun. Both surface currents and the wind are also influenced by what is known as the Coriolis effect.

The Coriolis Effect Because the earth is round and rotating, anything that moves over its surface tends to turn a little rather than moving in a straight line. One way to understand this bending, called the **Coriolis effect,** is to try a simple experiment. Put a piece of paper on a record turntable or some other rotating surface. Try to draw a straight line. The line will come out curved because the paper is spinning, moving under the pen. Figure 3.16 shows another way to understand the Coriolis effect.

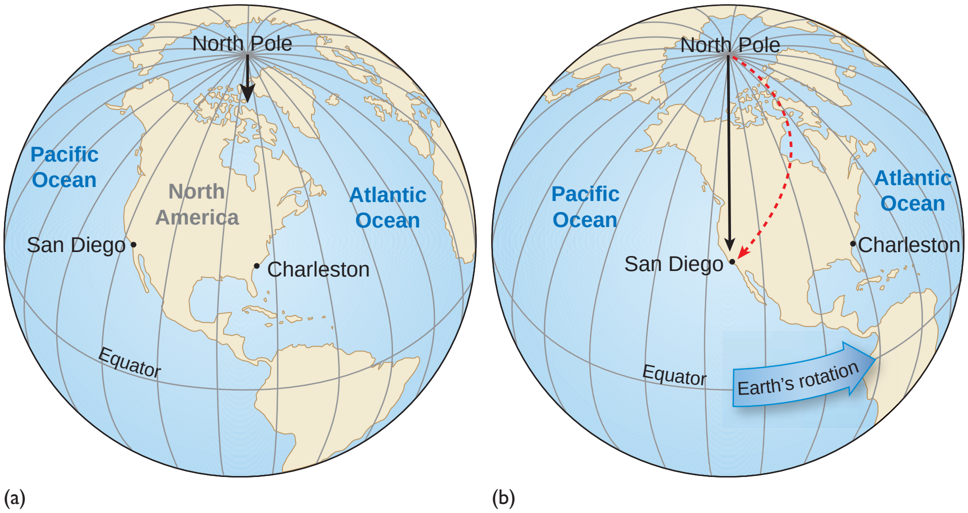


FIGURE 3.16 The Coriolis effect. (*a*) Imagine that someone fires a missile from the North Pole at Charleston, South Carolina. If the missile takes 2½ hours to reach its destination, (*b*) the earth will rotate under the missile while it is in the air so that the missile ends up hitting San Diego, California. From space it is clear that the missile moved in a straight line (black arrows) and the earth rotated, but to an observer on earth it would look like the missile curved (red arrow). The Coriolis effect would still apply if the missile was fired from east to west. Can you think of ways to explain this?

The Coriolis effect is too slight to notice when you're walking along or driving in a car, so most people aren't aware of it. It is very important, however, for things like winds and ocean currents that move over large distances. In the Northern Hemisphere the Coriolis effect always deflects things to the right. In the Southern Hemisphere, things are deflected to the left.

The Coriolis effect deflects large-scale motions like winds and currents to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.

Wind Patterns The winds in our atmosphere are driven by heat energy from the sun. The Equator is warmer than the poles because most of the sun's energy is absorbed near the Equator. As solar energy heats the Equator the air there becomes less dense and rises. Air from adjacent areas gets sucked in to replace the rising equatorial air, creating wind (Fig. 3.17). The winds do not move straight toward the Equator, but are bent by the Coriolis effect. These winds, called the **trade winds,** approach the Equator at an angle of about 45°. Over the ocean, where they are not affected by land, the trade winds are the steadiest winds on earth.

Other winds are also driven by solar energy but tend to be more variable than the trades. At middle latitudes lie the **westerlies** (Fig. 3.18), which move in the opposite direction to the trade winds. At high latitudes are the **polar easterlies,** the most variable winds of all.

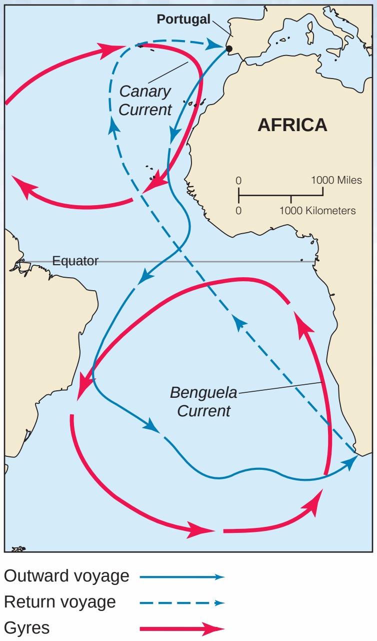
Surface Currents The major wind fields of the atmosphere push the sea surface, creating currents. All the major surface currents of the open ocean, in fact, are driven by the wind and ultimately by heat energy from the sun.

When pushed by the wind, the uppermost layer of surface water begins to move. Instead of going in the same direction as the wind, the surface current moves off at an angle of 45° because of the Coriolis effect (Fig. 3.19). This top layer pushes on the layer of water below, and again the Coriolis effect comes into play: The second layer moves not in the same direction as the top one, but slightly to the right, and slightly slower. This process passes down through the water column, each layer pushed by the layer above and pushing the one below, in a pattern called the **Ekman spiral** after the Swedish oceanographer who discovered it. The effect of the wind decreases with depth,

Tall Ships and Surface Currents

For purely practical reasons, winds and surface currents were among the first oceanic phenomena to be observed and documented. For centuries ships were at the mercy of the wind, and the names sailors gave to various areas reflected their knowledge of global wind patterns. Many of these names are still used. The trade winds got their name from the traders who relied on them during their voyages. The equatorial region where the winds are light and variable because of the rising air masses there (see Fig. 3.17) is called the doldrums. Winds are also variable at 30° north and south latitudes, where the trade winds and westerlies are moving apart (see Fig. 3.18). At these latitudes, sailors, becalmed and short of drinking water, sometimes had to throw their dying horses overboard. To this day these are known as the horse latitudes.

Sailors also knew about surface currents. A clever navigator could shorten a passage by weeks or months by riding favorable currents and avoiding unfavorable ones. In the fifteenth century, Portuguese sailors under the guidance of Prince Henry the Navigator made careful observations of currents along the west coast of Africa. Soon they were using their knowledge of these currents on their trading voyages. On the southbound journey, the ships sailed close to shore while in the Northern Hemisphere, riding the Canary Current. When they crossed the Equator they swung to the west to avoid the Benguela Current. On the voyage home, they took the opposite path, completing a figure eight.



The route of early Portuguese ships on trading voyages to the west coast of Africa. The southbound route is shown by a solid line, the northward journey by a dotted line. The prevailing currents are indicated by red arrows.

Early mariners knew about other currents as well. Christopher Columbus noted the existence of the North Atlantic Equatorial Current on his third voyage to the New World. While searching for the "Fountain of Youth" the Spaniard Juan Ponce de León described the Florida Current. In the Pacific, fishermen recorded their knowledge of the Perú Current and the Kuroshio.

Even Ben Franklin has a place in this story. While serving as deputy colonial postmaster he noticed that mail ships routinely made the trip to Europe two weeks faster than they returned. Upon questioning seafarers he learned of the mighty Gulf Stream and asked his cousin, a sea captain, to sketch it on a nautical chart. Franklin developed the sketch into the first published chart of the Gulf Stream, which is remarkably accurate. He understood that the Gulf Stream is a vast river of warm water flowing through the cold waters of the surrounding Atlantic Ocean and instructed ships to stay in the warm water of the Gulf Stream when sailing east but to avoid it on the westward journey. Later, on voyages as emissary to England, Franklin regularly measured sea temperature and published his findings in a report about the Gulf Stream.

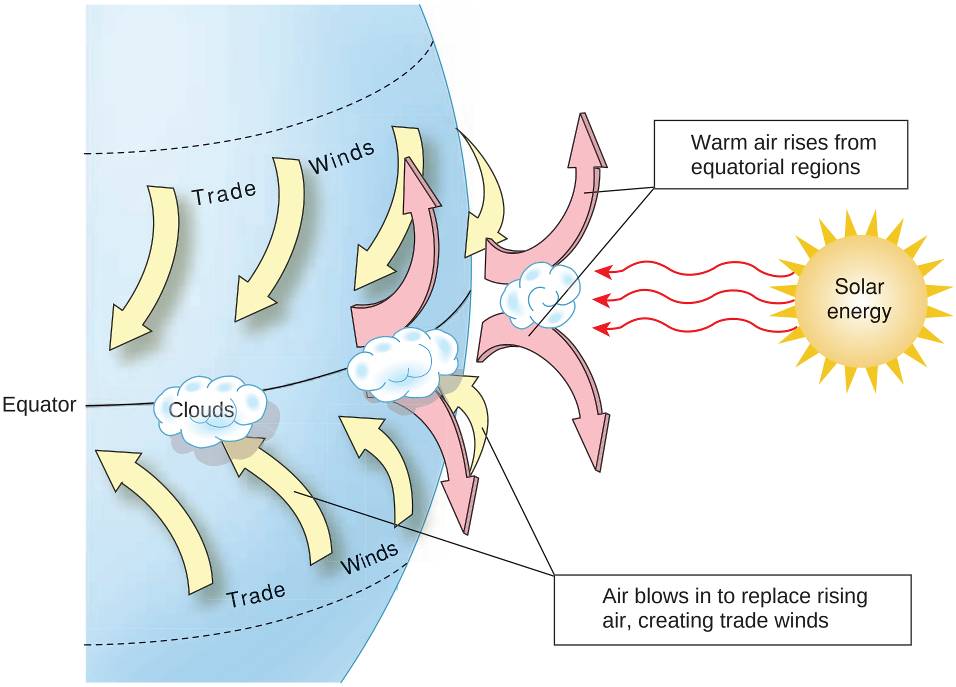

Trade
Winds
Warm air rises from equatorial regions
Solar energy
Equator
Clouds
Air blows in to replace rising air, creating trade winds
Trade
Winds

FIGURE 3.17 Air near the Equator is warmed by solar heating and rises. Air from higher latitudes moves in over the earth's surface to replace the rising air, creating wind. These winds, the trades, are deflected by the Coriolis effect and approach the Equator at an angle of about 45°.

so that progressively deeper layers move more and more slowly. Eventually, at a depth of at most a few hundred meters, the wind is not felt at all. The upper part of the water column that is affected by the wind is called the **Ekman layer.** Though each microlayer moves in a different direction, taken as a whole the Ekman layer moves at 90° from the wind direction. This process is called **Ekman transport.**

The Coriolis effect causes surface currents to move at 45° from the wind that drives them. Lower water layers move at progressively greater angles from the wind in a pattern called an Ekman spiral. This produces Ekman transport, in which the upper part of the water column moves perpendicular to the wind direction, to the right in the Northern Hemisphere and the left in the Southern Hemisphere.

A comparison of wind and surface current patterns demonstrates the consequences of the Coriolis effect. While the trade winds move toward the Equator, for example, the **equatorial currents** that these winds produce move parallel to the Equator (Fig. 3.20). Under the influence of the Coriolis effect, the wind-driven surface currents combine into huge, more or less circular systems called **gyres.**

Recall that water is particularly good at transporting heat because of its high heat capacity. The warm currents on the western sides of the gyres carry vast

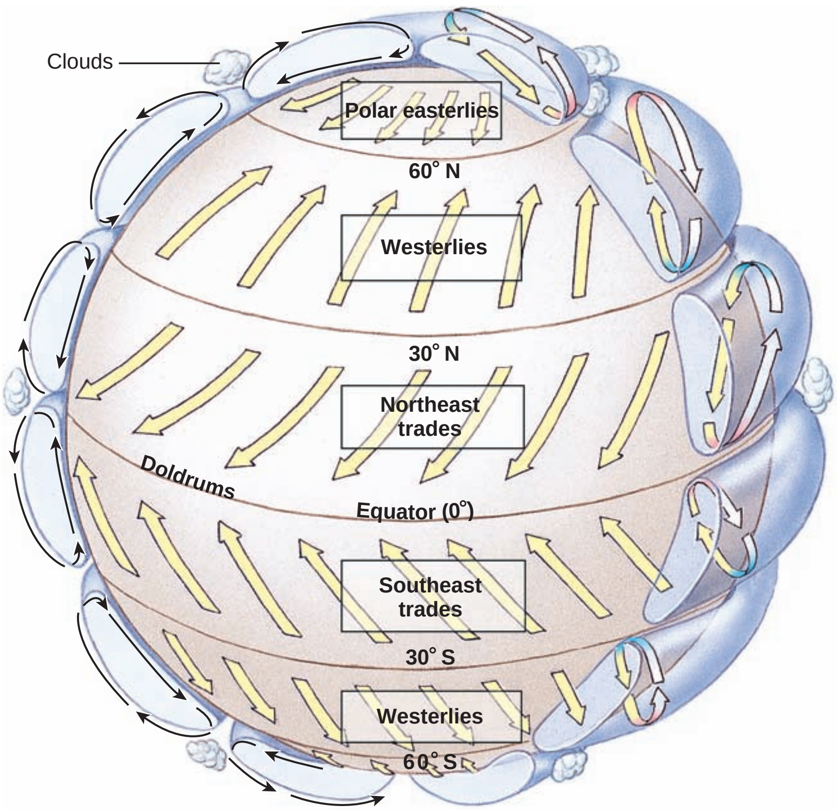

Clouds
Polar easterlies
60° N
Westerlies
30° N
Northeast trades
Doldrums
Equator (0°)
Southeast trades
30° S
Westerlies
60° S

FIGURE 3.18 The major wind patterns on earth are created by the rising of sun-warmed air and the sinking of cold air. The trade winds lie between about 30° north and south latitude and are the steadiest of all winds. The westerlies are found from about 30° to 60°, and above 60° lie the most variable winds, the polar easterlies. The transition zones or boundaries between these major wind belts have very light and changeable winds (see "Tall Ships and Surface Currents," p. 50). The wind fields are pictured here as they would look on an imaginary water-covered earth. In actuality they are modified by the influence of the continents (see Fig. 3.20).

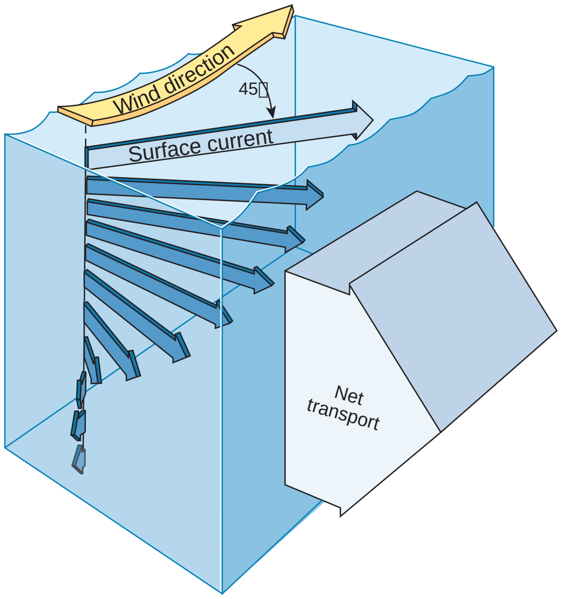

Wind direction
45°
Surface current
Net transport

FIGURE 3.19 When a steady wind blows over the sea surface, the uppermost layer moves at 45° from the wind direction. Each deeper layer moves farther to the right in the Northern Hemisphere, shown here, or to the left in the Southern Hemisphere. When the direction of the current at each depth is plotted, the result is a spiral, called the Ekman spiral. The net result of this process is that the affected layer of water, called the Ekman layer, is transported at right angles to the wind direction.

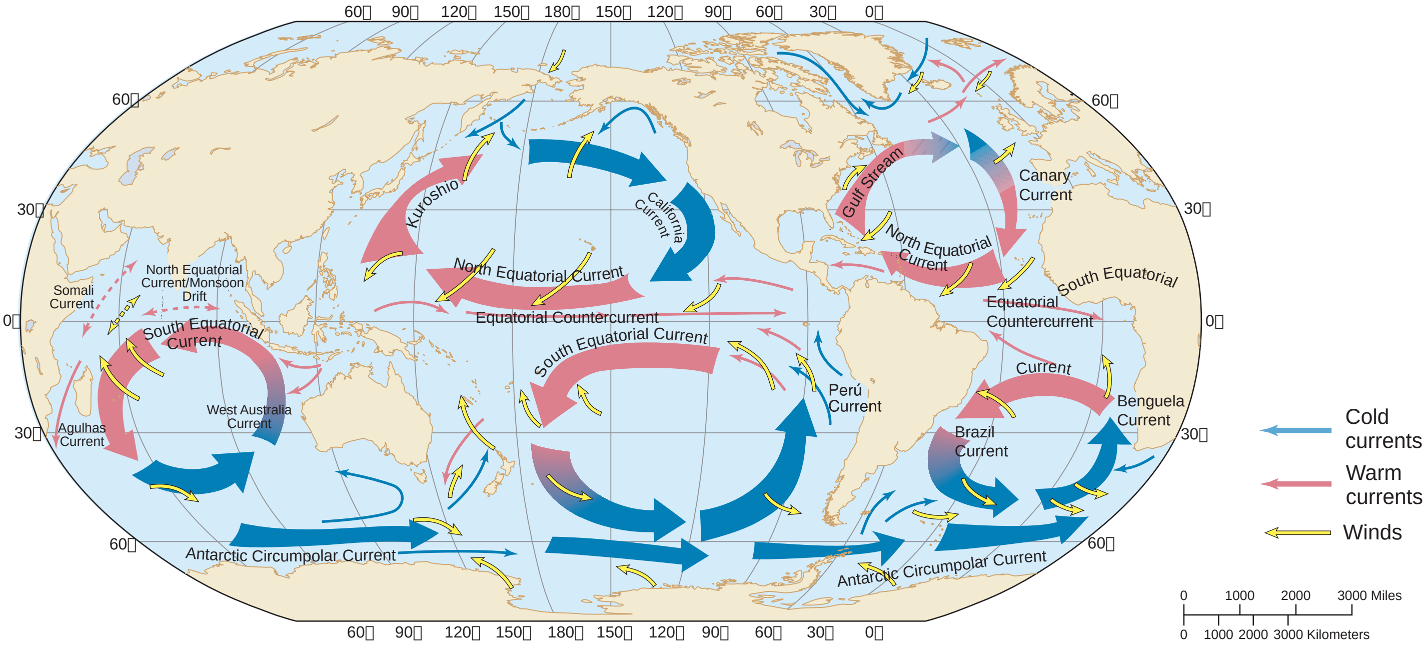
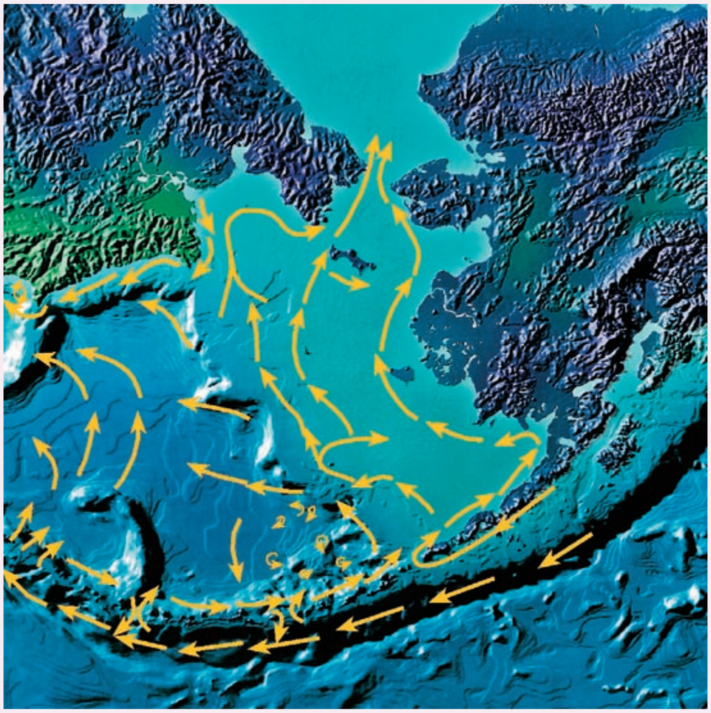

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60°
30°
0°
30°
60°
Kuroshio
California Current
North Equatorial Current
Equatorial Countercurrent
South Equatorial Current
Gulf Stream
Canary Current
North Equatorial Current
Equatorial Countercurrent
South Equatorial Current
Somali Current
North Equatorial Current/Monsoon Drift
South Equatorial Current
West Australia Current
Agulhas Current
Perú Current
Brazil Current
Benguela Current
Antarctic Circumpolar Current
Antarctic Circumpolar Current
Cold currents
Warm currents
Winds
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers

FIGURE 3.20 The major surface currents of the oceans. In the main ocean basins the currents combine to form large circular systems called gyres.

EYE ON SCIENCE

The Bering Sea Ecosystem Study

The Bering Sea is one of the world's richest fishing grounds and produces more than half the commercial catch in the United States, as well as subsistence catches to indigenous peoples in both North America and Asia. The rich and diverse ecosystem supports whales, seals, walrus, and other marine mammals and huge numbers of seabirds (including 80% of seabird species in U.S. waters). The oceanography of the area is also of great interest: A flow of seawater from the Pacific Ocean through the Bering Sea into the Arctic Ocean helps regulate Arctic climate and may influence the earth's entire climate system. It also helps regulate the nutrient balance of the northern Atlantic and Pacific oceans.


Current patterns in the Bering Sea.

But the Bering Sea is changing. Fisheries have been in decline after a peak in 1990, and since the late 1990s several salmon runs have collapsed. Populations of seabirds and marine mammals, including the northern fur seal (*Callorhinus ursinus*) and Steller sea lion (*Eumetopias jubatus*), are decreasing. Jellyfish numbers rose dramatically during the 1990s, then crashed early in this century. Massive plankton blooms showed a similar pattern, appearing annually from 1997 to 2001 and then disappearing. The entire ecosystem seems to be undergoing a fundamental shift. The reasons are unknown, but could be related to a decline in sea ice and a general warming of the Arctic (see "What's Happening Now?," p. 233).

The Bering Sea Ecosystem Study (BEST) seeks to reveal the causes and consequences of these changes. The initial priorities of the study focus on the effects of global warming: What are the effects of decreased seasonal sea ice and increased warming of surface waters on the sea's productivity, nutrient balance, and other aspects of its ecology?

BEST will require the use of multiple ships and the long-term deployment of a variety of instruments, coupled with remote sensing, mathematical modeling, and laboratory analyses. Oceanographers, climatologists, chemists, biologists, and other scientists from many institutions in several countries will work together. Social scientists will study the impact of change in the Bering Sea on the people who use it. Thus, there will be as many logistical problems as scientific ones. Work in the sea ice, frigid temperatures, and ferocious storms of winter will be a major challenge—a lack of wintertime data is one the main information gaps. BEST is now in the process of ironing out where the ships will come from, who will do what when, how best to store and share information, and how to pay for it all, in the hope that BEST ships will leave port in 2007.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

amounts of solar heat from the Equator to higher latitudes. Cold currents flow in the opposite direction on the eastern sides. Ocean currents thus act like a giant thermostat, warming the poles, cooling the tropics, and regulating the climate of our planet. Large-scale fluctuations in current patterns such as El Niño can dramatically affect weather around the world (see "The El Niño–Southern Oscillation Phenomenon," p. 353).

The role of surface currents in transporting heat is reflected in the temperature of the sea surface (Fig. 3.21). Surface temperature is higher on the western sides of the oceans, where currents carry warm water away from the Equator, than on the eastern sides, where cold currents flow toward the Equator. Because of this, tropical organisms like corals tend to extend into high latitudes on the west sides of the oceans (see "Conditions for Reef Growth," p. 308, and Fig. 14.11). Cold-loving organisms like kelps, on the other hand, occur closest to the Equator on the eastern shores of the oceans (see "Kelp Communities," p. 296, and Fig. 13.22).

Global wind patterns and the Coriolis effect produce gyres, large circular systems of surface currents. These currents regulate the earth's climate by transporting heat from tropical to polar regions and greatly affect the geographic distribution of organisms in the ocean.

The currents shown in Figure 3.20 are average patterns over large distances and a long time span. At a given place on a given day the current is often different: Currents shift with the season and the weather. On the continental shelf, currents are strongly affected by the bottom, the shape of the coastline, and the tides (see "Physical Characteristics of the Subtidal Environment," p. 283).

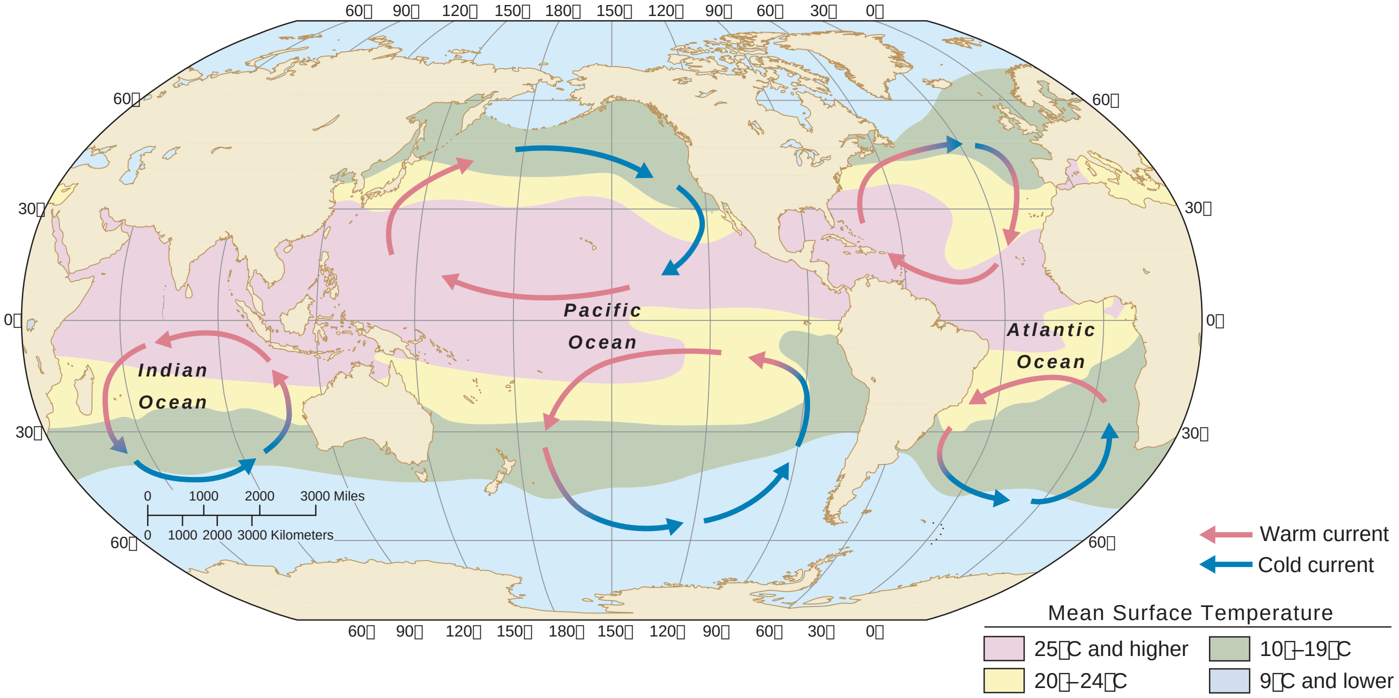


FIGURE 3.21 The average sea-surface temperatures of the oceans are strongly affected by the ocean gyres.

Thermohaline Circulation and the Great Ocean Conveyor

The ocean is a three-dimensional habitat, and the major currents shown in Figure 3.20 reflect circulation only at the surface, not at greater depths. Over much of the ocean, surface waters are partially isolated from deeper waters by differences in density, which is why oceanographers painstakingly measure the two factors—temperature and salinity—that determine seawater density.

Because the densest water sinks, the ocean is usually layered, or **stratified,** with the densest water on the bottom and the least dense at the surface. This can be seen in typical profiles of salinity, temperature, and density (Fig. 3.22). Deep water is normally cold and dense, whereas the surface water is relatively warm and "light."

> The water column in the ocean is usually stratified, with the least dense water at the surface and the densest water on the bottom.

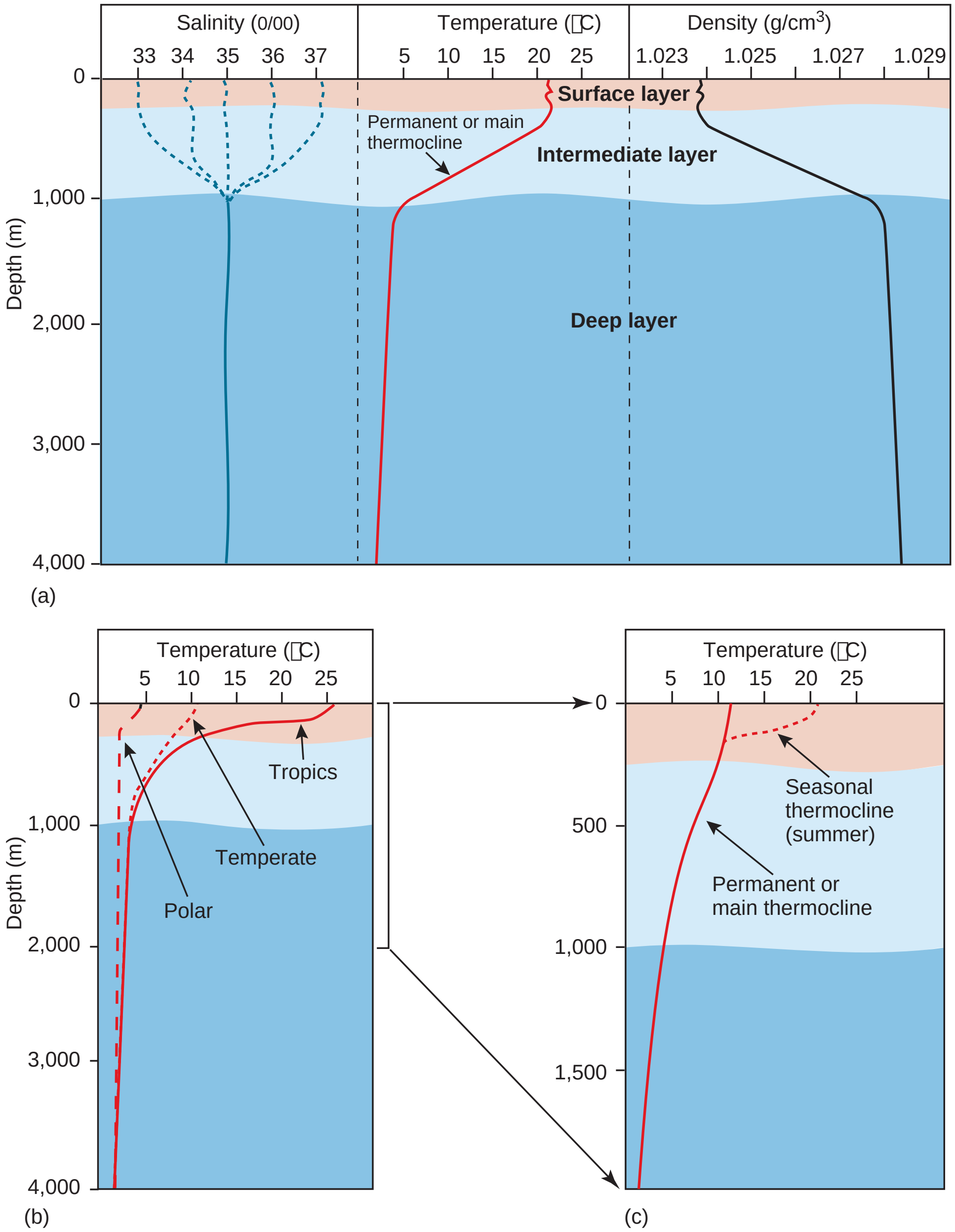
The Three-Layered Ocean Although there are actually many thin layers of water, each of slightly different density, it is not a bad approximation to view the ocean as having three principal layers (Fig. 3.22*a*). The **surface layer** is usually around 100 to 200 m (330 to 660 ft) thick. Much of the time the surface layer is mixed by wind, waves, and currents, so it is also known as the **mixed layer.** The surface layer is not always well mixed, however. Sometimes, usually in the spring and summer in temperate and polar water, the very uppermost part of the surface layer gets heated by the sun. The warm water floats in a shallow "lens" on top, and there is a sharp transition to the cooler water below. These sudden changes in temperature over small depth intervals, called **thermoclines,** are often noticed by divers. When the weather becomes colder, wind and waves again mix the water column and these temporary shallow thermoclines break down.

The **intermediate layer** lies below the surface layer, typically to a depth of 1,000 to 1,500 m (3,300 to 5,000 ft). The **main thermocline,** a zone of transition between warm surface water and the cold water below, lies in the intermediate layer. The main thermocline should not be confused with the much shallower, seasonal thermoclines in the surface layer. The main thermocline rarely breaks down, and then only in a few places. The main thermocline is a feature of the open ocean. The waters over the continental shelf are not deep enough to have a main thermocline; in shelf waters the mixed surface layer often extends all the way to the bottom.

Below about 1,500 m (5,000 ft) lie the **deep** and **bottom layers.** Technically, deep water and bottom water are different, but they are similar in being uniformly cold, typically less than 4°C (39°F).

> The ocean has three main layers: the surface or mixed layer, the intermediate layer, and the deep layer.

Stability and Overturn Most of the time surface water, being warmer and less dense, floats on top of the denser water below unless wind or wave energy stirs up the water column. Such a water column is said to be **stable.** *How* stable the water column is depends on the density difference between the layers. When the surface layer is only slightly less dense than the layer below, less energy is required to mix the two layers and the water column has low stability. A highly stable water column, on the other hand, results from a large density difference



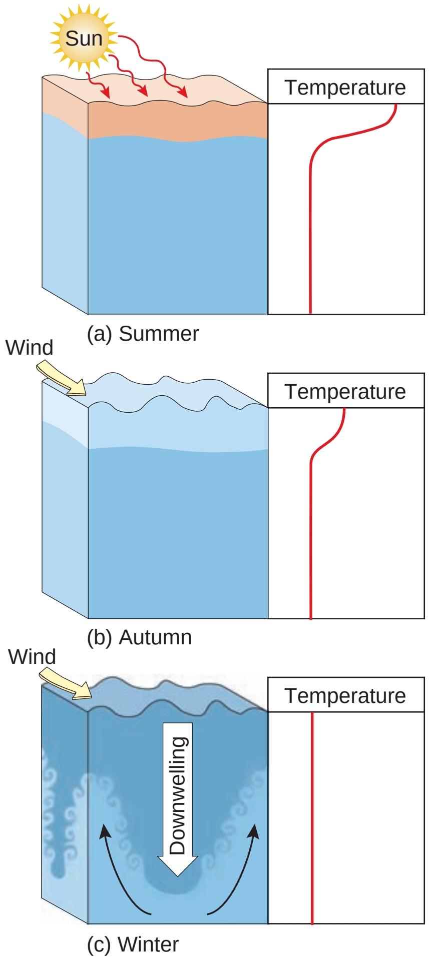


FIGURE 3.23 (*a*) In temperate and polar regions the summer sun warms the surface layer, making it much less dense than the water below. (*b*) In autumn the surface water begins to cool, and storm winds mix colder deep water to the surface. (*c*) If the surface water gets cold enough, which usually happens in winter, it becomes denser than the deeper water and sinks, which is called downwelling. The deeper water is displaced to the surface, and the entire process is known as overturn.

FIGURE 3.22 (*a*) Typical profiles of salinity, temperature, and density in the open ocean. Salinity profiles near the surface vary considerably because of precipitation, evaporation, and river runoff. Temperature and density profiles are usually mirror images of each other because temperature largely controls seawater density. Surface water is usually warmer and therefore less dense than the water below. (*b*) The temperature of the surface, as you might expect, varies with latitude, with the highest surface temperature occurring in the tropics. Deep-water temperature and salinity is much more uniform. (*c*) In temperate and polar waters, seasonal thermoclines may develop in the surface layer during the summer when the sun warms the uppermost part of the water column. Note that the depth scale in (*c*) is different from that in (*a*) and (*b*).

between deep and shallow water, and requires much more energy to mix.

Sometimes water columns become unstable, meaning that the surface water becomes more dense than the water below. The surface water sinks, which is called **downwelling,** and displaces and mixes with deeper water. This process is known as **overturn** (Fig. 3.23). Because surface water, all with the same temperature and density, is descending through the water column, the temperature and density profiles are vertical straight lines, and oceanographers identify conditions of overturn by looking for such straight-line profiles. Overturn usually occurs in temperate and polar regions during the winter when the surface water cools.

When overturn occurs over only a small area or when the surface water is only slightly denser than the water below, the downwelling water simply mixes with deeper water, so that the mixed layer extends deeper in the water column. This mixing is important for the productivity of temperate and polar waters (see “Patterns of Production,” p. 346). When downwelling is intense, however, a large volume of water may leave the surface without mixing much with the surrounding water. The processes that change salinity in the open ocean—precipitation, evaporation, and freezing—occur only at the surface. Temperature also changes primarily at the surface, through evaporative cooling, solar heating, or the exchange of heat with the atmosphere. Once surface water has sunk, therefore, its salinity and temperature do not change. From then on the volume of water, or **water mass,** has a "fingerprint," a characteristic combination of temperature and salinity. Oceanographers can use this to follow the movement, or **circulation,** of water masses over great distances. Because this form of circulation is driven by changes in density, which in turn is determined by temperature and salinity, this form of circulation is known as **thermohaline circulation.**

The Great Ocean Conveyor After water masses leave the surface they sink to a depth determined by their density. Water of intermediate density descends only part way, to a depth where it is denser than the water above but less dense than the water below. To sink all the way to the bottom of the ocean, surface water must become very dense—that is, cold and relatively salty. This occurs at only a few locations, and only intermittently. The main places where surface overturn reaches the bottom are in the Atlantic Ocean, south of Greenland and just north of Antarctica (Fig. 3.24). After sinking, the water spreads through the Atlantic and into the other ocean basins. The water eventually rises to the surface and flows back to the Atlantic, where the cycle begins again (Fig. 3.25). This global thermohaline circulation, called the **great ocean conveyor,** mixes the oceans on a timescale of about 4,000 years. The great ocean conveyor is also critical in regulating the earth's climate, and it is thought that alterations in the conveyor have produced rapid climate changes, even ice ages, in the past. The conveyor also brings dissolved oxygen to the deep sea (see "The Oxygen Minimum Zone," p. 367). This effect is enhanced because oxygen dissolves best in cold water (see "Dissolved Gases," p. 47).

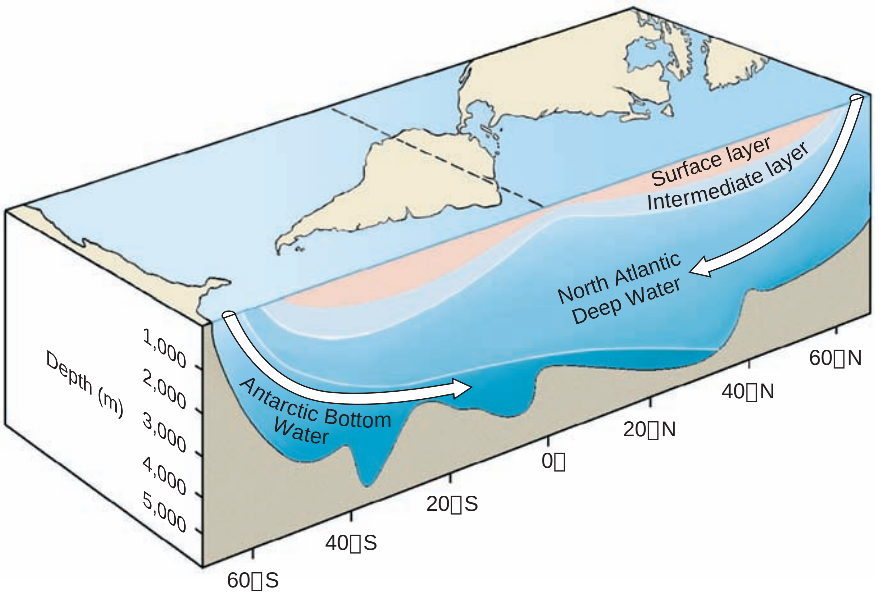


FIGURE 3.24 The deepest water in the deep and bottom layers of the Atlantic Ocean consists largely of two large water masses called North Atlantic Deep Water and Antarctic Bottom Water. These water masses originate at the surface in the extreme North and South Atlantic, respectively, then sink and spread along the bottom. Deep water originating in the Atlantic also spreads to the other ocean basins (see Fig. 3.25).

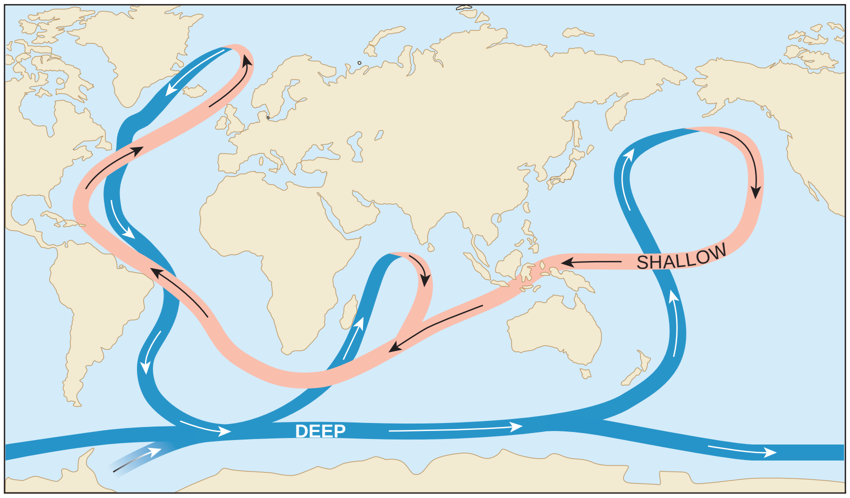


FIGURE 3.25 The deep circulation of the oceans is part of a global pattern known as the great ocean conveyor. This circulation constantly replenishes the oxygen supply to the ocean depths. Small variations in the conveyor circulation are thought to produce dramatic changes in weather patterns around the world. Larger changes may even bring on ice ages.

WAVES AND TIDES

The great ocean currents, as important as they are, aren't usually apparent to the casual observer. Waves and tides, on the other hand, are among the most visible of all ocean phenomena. Anyone who has swum in, sailed on, or simply walked beside the sea is familiar with waves and tides.

Waves

The wind not only drives surface currents, it causes **waves.** The highest part of a wave is called the **crest** and the lowest part the **trough** (Fig. 3.26). The size of an ocean wave is usually expressed as the wave **height,** which is the vertical distance between the trough and the crest. Wave crests or troughs can be close together or far apart. The distance between them is called the **wavelength.** The time a wave takes to go by any given point is called the **period** of the wave.

When under a wave crest the water moves up and forward; under the troughs it moves down and back. On the whole the water particles don't go anywhere at all as the wave passes; they just move in circles (Fig. 3.27). Though waves carry energy across the sea surface, they do not actually transport water.

Waves begin to form as soon as the wind starts to blow. The faster and longer the wind blows, the larger the waves get.

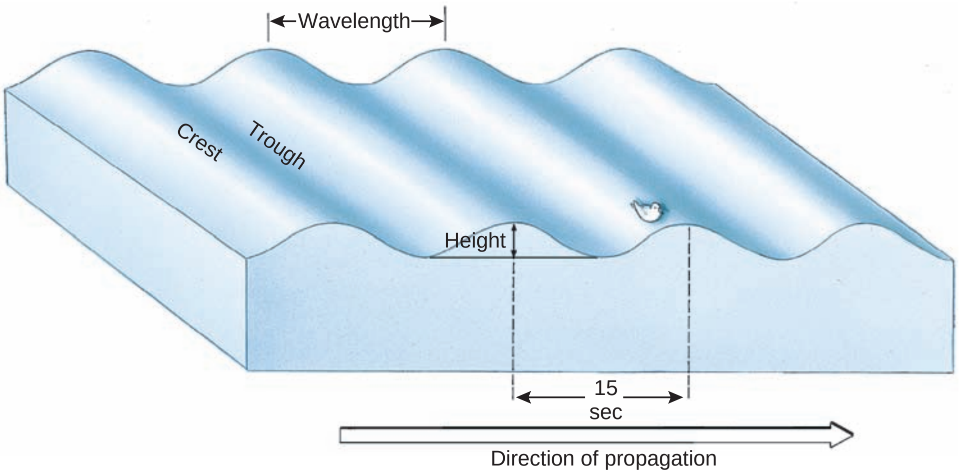


FIGURE 3.26 An idealized series of waves, or wave train. The highest point of a wave is called the crest, the lowest point the trough. The wavelength is the distance between crests. The wave period refers to how long it takes the wave to go by. In this example the period is 15 seconds, which is how long it will take for the next crest to reach the bird.

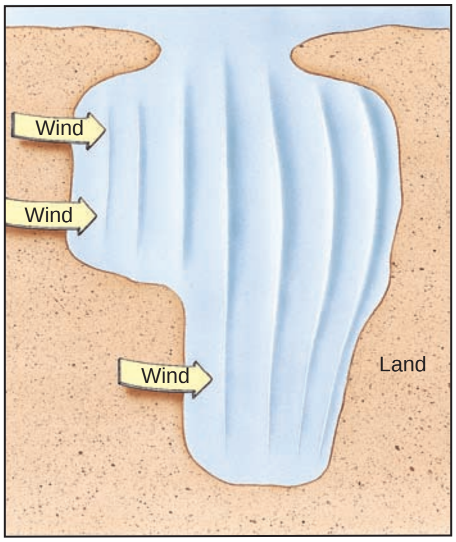


FIGURE 3.28 The wind is blowing at the same speed and has been blowing for the same length of time over this entire imaginary bay. On the top side of the bay, however, the wind is blowing over a much longer stretch of water. In other words, the fetch is longer on the top side, so the waves are bigger there.

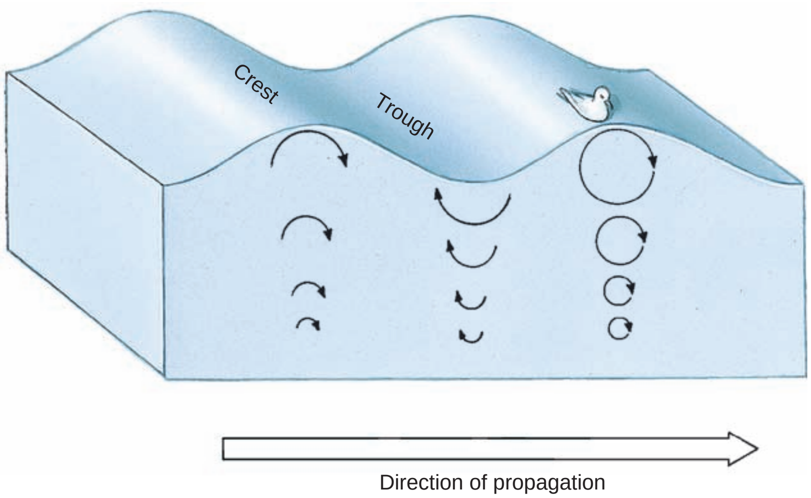


FIGURE 3.27 Water particles do not move along with a wave but instead move in circles. When under the crest they move up and forward with the wave, then they are pulled back down. As wave after wave passes, the water and anything floating in or on it moves in circles.

The size of waves generated by the wind also depends on the **fetch,** the span of open water over which the wind blows (Fig. 3.28).

While the wind is blowing it pushes the wave crests up into sharp peaks and "stretches out" the troughs (Fig. 3.29). Waves like this are called **seas.** The waves move away from where they are generated slightly faster than the speed of the wind. Once away from the wind the waves settle into **swells.** With their smoothly rounded crests and troughs, swells are very similar to the ideal waves shown in Figure 3.26.

When the waves approach shore and get into shallow water, they begin to "feel" the bottom. The bottom forces the water particles to move in elongated ellipses instead of circles, which slows the wave. As the waves behind catch up the waves get closer together, giving them a shorter wavelength. The waves "pile up," becoming higher and steeper. Eventually they become so high and so steep that they fall forward and break, creating **surf.** The energy that was put into the wave by the wind is expended on the shoreline as the wave breaks.

The sea surface is usually a confused jumble instead of a series of nice, regular waves moving in one direction. This is because the surface at any given location is affected by a mixture of waves coming from many different places, generated by winds of different speeds blowing in different directions for different lengths of time. The complex surface of the ocean results from the interactions of all these waves. **Wave cancellation** occurs when the crest of one wave meets the trough of another, and the sea surface ends up intermediate between the two. If the crests of two waves collide, however, they add together to produce a higher wave. This **wave reinforcement** occasionally produces rogue waves as tall as a 10-story building that seem to come up out of nowhere. Oceanographers once dismissed rogue waves as rare or even nonexistent, nothing more than sailors' myth. Recent satellite observations, however, have confirmed that rogue waves do occur. They may account for a significant fraction of the 100 or so large ships lost at sea every year.

Tides

The sea surface has been rising and falling in the rhythmic pattern known as the **tides** for billions of years. The tides are a dominant influence on nearshore sea life. They alternately expose and submerge organisms on the shore (see Chapter 11), drive the circulation of bays and estuaries (see Chapter 12), trigger

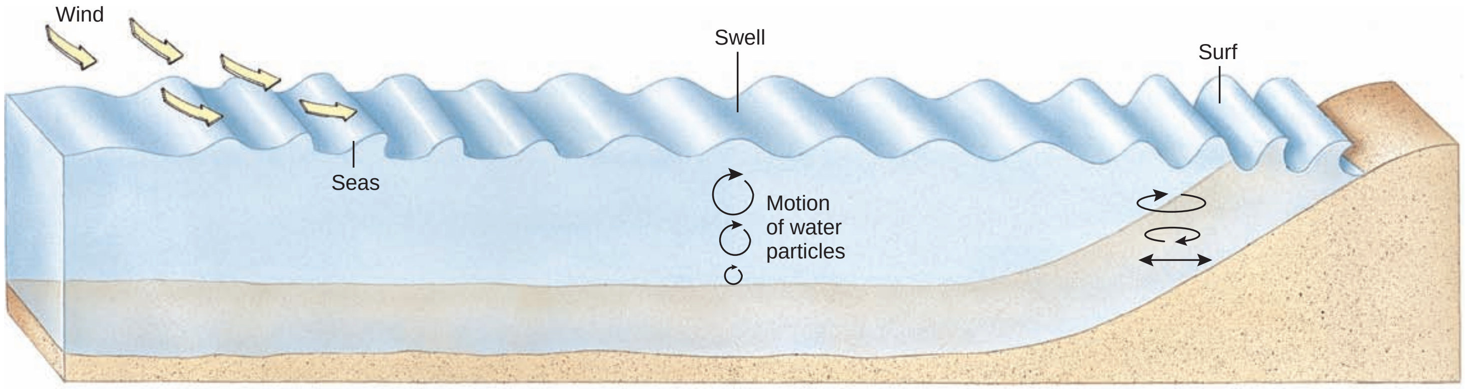


FIGURE 3.29 Storm winds generate seas, peaked waves with relatively flat troughs. The waves move out of the storm area, carrying energy away, and become swells, with rounded crests and troughs. When the waves reach shallow water, they get higher and shorter, that is, closer together. Eventually they become unstable and break, expending their energy on the shoreline. Water particles under swells have the ideal circular motion shown in Figure 3.27. In shallower water the influence of the bottom causes the particle motion to flatten out into a back-and-forth movement known as surge.

spawning (Fig. 3.30), and influence the lives of marine organisms in countless other ways.

Why Are There Tides? The tides are caused by the gravitational pull of the moon and sun and by the rotations of the earth, moon, and sun. The moon and earth are held together by gravitational attraction. The moon's gravity is strongest on the side of the earth closest to the moon. Here the moon's gravity pulls the water in the ocean toward the moon, so that if the earth were covered entirely by water the ocean would bulge toward the moon (Fig. 3.31). On the opposite side of the earth, further away from the moon, the moon's gravitational pull is weaker, so the water does not move toward the moon. In fact, it bulges in the opposite direction, away from the moon, because of centrifugal force. This centrifugal force arises because, strictly speaking, the moon does not revolve around the earth. Instead, the earth and moon both rotate around their combined center of mass, which lies inside the earth but offset slightly from the actual center of the earth (Fig. 3.31). This offset causes the earth-moon system to wobble slightly, like an unbalanced tire, and creates a centrifugal

FIGURE 3.30 These grunion (*Leuresthes tenuis*) are laying eggs high on a California beach. Their spawning is precisely timed to coincide with the peak of the highest tides, when they can reach the uppermost parts of the beach. Hatching of the eggs, not quite a month later, also corresponds to high tides so that the fry can swim away.

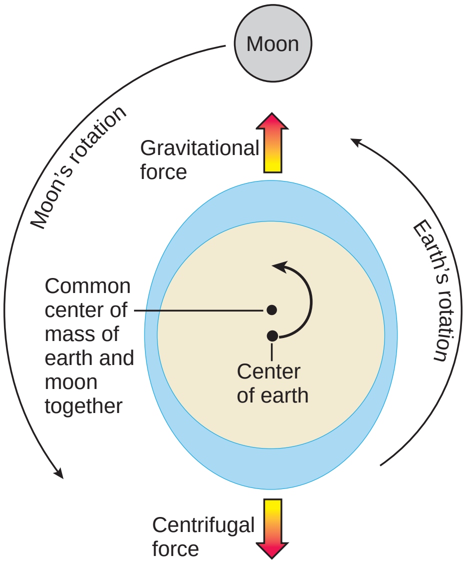


FIGURE 3.31 The moon does not exactly rotate around the earth. Instead, both the moon and earth rotate around their common center of mass, which lies inside the earth. Thus, the earth actually "wobbles" a bit, like an unbalanced tire. Centrifugal force produced by the earth's motion causes the water to bulge outward, away from the moon. On the side of the earth closest to the moon, however, the moon's gravitational pull overcomes the centrifugal force and pulls the water into a bulge *toward* the moon.

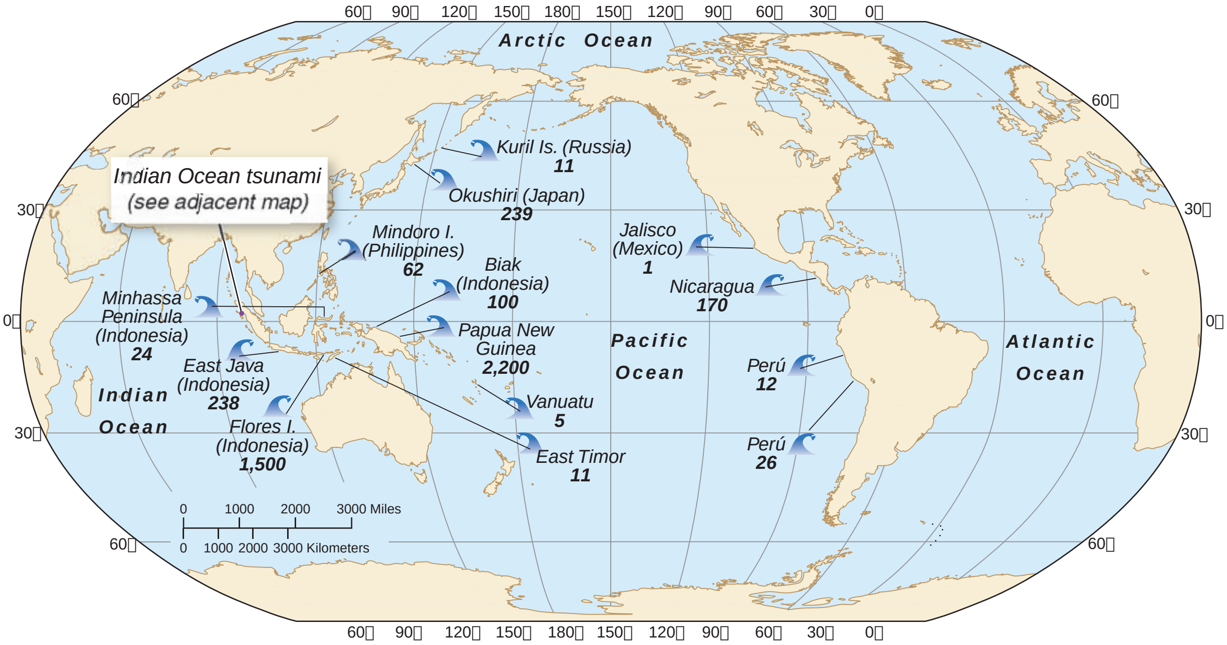
Waves That Kill

Every surfer or beachgoer who has been "barrel rolled" knows how much force a breaking wave can deliver, but waves are usually pretty harmless. Occasionally, however, killer waves unleash all the awesome power of the sea. Every year, violent storm waves damage coastal areas somewhere, and sometimes even kill people. Rogue waves (see "Waves," p. 55) cause an unknown number of casualties.

The deadliest waves by far are **tsunamis,** a Japanese word meaning "harbor waves." Sometimes called tidal waves, tsunamis have nothing to do with the tides. They are produced by earthquakes, landslides, volcanoes, and other seismic disturbances of the sea floor, so they are also called seismic sea waves. Tsunamis are much longer and travel much faster than ordinary wind waves. They can have wavelengths of 240 km (150 mi) and travel at over 700 km/hr (435 mi/hr)—as fast as a jet. In the open ocean, tsunamis are not very high, usually less than 1 m (40 in), and are hardly noticeable. They get higher when they approach shore, but this increase is generally minor and most tsunamis do little damage.

Once in a while, though, a tsunami is huge and causes great death and destruction. In 1883 the volcanic island of Krakatoa in the Indian Ocean exploded, causing tsunamis around half the globe that killed more than 35,000 people. Fatal tsunamis occur every year or two on average, especially in the Pacific where about 85% of all tsunamis occur because of seismic activity around the Pacific Rim. Hawai'i suffered a tsunami in 1946 that took 159 lives and another in 1960, the result of an earthquake in Chile, left 61 dead on the island. The west coast of the United States also suffered deadly tsunamis as a result of both the 1960 Chile earthquake and the great Alaskan earthquake of 1964. A 1998 tsunami in Papua New Guinea left 2,200 known dead and thousands missing. Many other parts of the world have also been hit. Between 1992 and 2002 tsunamis caused more than 4,000 known deaths, and the true toll is probably higher because casualties are often not accounted for.

The deadliest tsunami in recorded history, struck in the Indian Ocean. On 26 December 2004, a huge piece of the Indian Plate slid under the Burma Plate off the northeast coast of the Indonesian island of Sumatra. This generated an earthquake of at least 9.0 on the Richter scale, the strongest since the 1964 Alaskan quake. The earthquake in turn sent a tsunami racing across the Indian Ocean. Within minutes waves at least 10 m (30 ft) high—estimates range as high as 30 m (100 ft)—smashed onto the coast of Aceh, the part of Sumatra nearest the quake. Aceh suffered the worst devastation and greatest loss of life, but in less than eight hours the tsunami hit coastal areas around the Indian Ocean, killing an estimated 230,000 people in 12 countries. In addition to the terrible death toll, millions of families were left homeless. Schools, hospitals, and indeed entire towns disappeared. Resorts, stores, restaurants, factories, and other businesses were washed away, taking precious livelihoods with them. Ports and boats were smashed, and road, water, electricity, communication, irrigation, and other networks wiped out. Farmland, wells, and groundwater supplies were inundated with seawater, and the grim catalog of damage goes on and on. The blows were especially cruel because many of the affected areas were


60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
Arctic Ocean
60°
30°
0°
Kuril Is. (Russia)
11
Okushiri (Japan)
239
Indian Ocean tsunami
(see adjacent map)
Mindoro I.
(Philippines)
62
Biak
(Indonesia)
100
Jalisco
(Mexico)
1
Nicaragua
170
Minhassa
Peninsula
(Indonesia)
24
Papua New
Guinea
2,200
Pacific
Ocean
Atlantic
Ocean
Perú
12
East Java
(Indonesia)
238
Indian
Ocean
Vanuatu
5
Flores I.
(Indonesia)
1,500
East Timor
11
Perú
26
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers

Worldwide death toll from tsunamis between the years 1992 and 2002. These figures are probably underestimates.

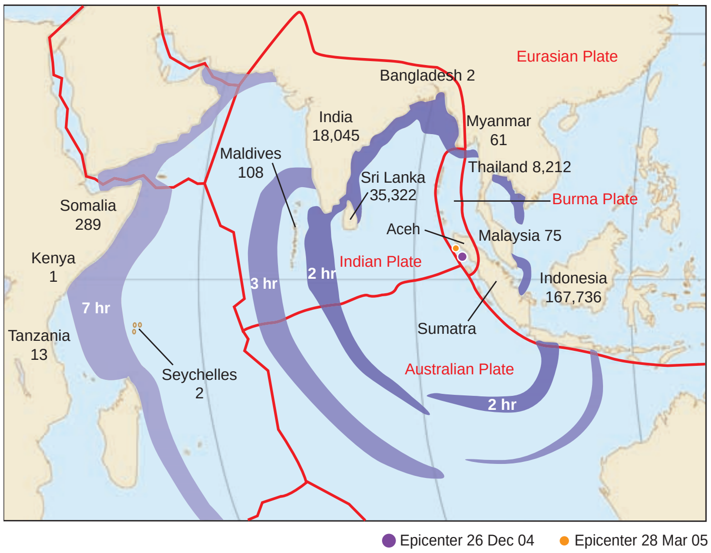
already desperately poor, and a return even to what little prosperity there was may take decades.

The tsunami also inflicted considerable damage to coastal marine habitats, including coral reefs, mangrove forests, and seagrass beds. Under natural conditions these habitats would recover, but unfortunately many of them have been badly degraded by human activities (see "Human Impacts on Estuarine Communities," p. 281, and "Coral Reefs," p. 403). This is sadly ironic, because mangroves and coral reefs help protect the coastline, and tsunami damage was reduced in the few places where these habitats were intact.

Not much could have been done to prevent the physical damage, but many lives would have been saved if people in vulnerable areas had been warned to move to higher ground. A tsunami warning system was developed for the Pacific following the deadly tsunamis of 1960 and 1964, but a system for the rest of the world had only been discussed. The earthquake that spawned the Indian Ocean tsunami was detected by a seismic station in Hawai'i almost immediately, but there was no way to get word out to where it was needed. Thousands of lives were saved in the few instances when someone did happen to notice an Internet posting or get a phone call, but these cases were all too few.

Within weeks the international community started in earnest to establish a global tsunami warning system, prodded not only by the horror of the 26 December tsunami but also by predictions of more earthquakes in the area due to continued stress along the plate boundary. Only three months later, in fact, a second major earthquake (magnitude 8.7) occurred nearby. This time governments swiftly issued warnings and in some places ordered the evacuation of low-lying areas. The earthquake itself killed about 2,000 people, but there was no tsunami. This demonstrates a major problem: Seismic stations detect major earthquakes almost immediately, but scientists are still unable to accurately predict which earthquakes will generate a tsunami. Therefore, the tsunami warning system being established in the Indian Ocean relies on permanent, moored buoys that can detect the waves themselves and transmit warnings via satellite.

The best protection against tsunamis may be education. The first wave of the 26 December tsunami, for example, was relatively small and if people had been aware that it might signal more destructive waves to follow they could have moved inland. In many places the water receded out to sea in front of the destructive second wave, another common sign of an impending tsunami. There were newspaper reports of a 10-year-old remembering this from a school lesson and saving hundreds of people on a beach in Thailand. In most places, though, the warning went unheeded. As often happens, in fact, many people went further out on the beach to investigate, sealing their fates.



The progress of the leading wave of the Indian Ocean tsunami of 26 December 2004 and the resultant toll of dead and missing. As with many other tsunamis, there was actually a series of waves rather than a single one, just as tossing a rock into a pond creates more than one wave. Most places were hit by three waves, with the second being the most destructive.

Tsunami survivors pick through rubble in Banda Aceh, Indonesia.

force that pushes water away from the moon. Thus, on a water-covered earth the water would form two bulges on opposite sides of the planet, one bulge toward the moon where the moon's gravity predominates and the other bulge away from the moon where centrifugal force predominates. The water would be relatively deep under the bulges and shallow away from the bulges.

In addition to the rotation of the earth and moon illustrated in Figure 3.31, the earth is spinning like a top on its own axis. As it does so, any given point on the planet's surface will alternately lie under a bulge and then away from it (Fig. 3.32). High tide occurs when the point is under a bulge. Because the earth takes 24 hours to complete a rotation, the point will have two high tides and two low tides every day. Actually, the moon advances a little in its own orbit in the course of 24 hours. It takes the point on earth an extra 50 minutes to catch up and come directly in line with the moon again. A full tidal cycle therefore takes 24 hours and 50 minutes.

The sun produces tidal bulges in the same way as the moon. Though the sun is much larger than the moon, it is 400 times farther away, so the effect of the sun on the tides is only about half as strong as the moon's. When the sun and moon are in line with each other, which happens at the full and new moons (Fig. 3.33), their effects add together. At these times the **tidal range,** or difference in water level between successive high and low tides, is large. Such tides are called **spring tides** because they seem to surge up like a spring of water. The name has nothing to do with the season; spring tides occur throughout the year.

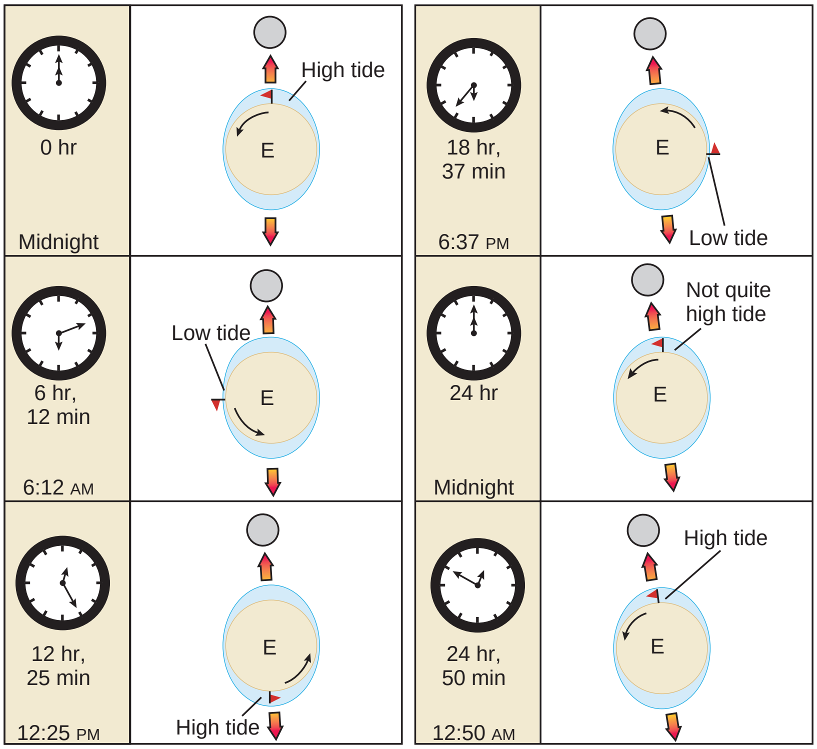

0 hr
Midnight
High tide
E
18 hr, 37 min
6:37 PM
E
Low tide
6 hr, 12 min
6:12 AM
Low tide
E
24 hr
Midnight
Not quite high tide
E
12 hr, 25 min
12:25 PM
E
High tide
24 hr, 50 min
12:50 AM
High tide
E

FIGURE 3.32 As the earth spins on its axis, a given point on earth like the one marked by the flag alternates between being under a bulge, making it high tide, and being between the bulges, making it low tide. Because the moon moves while the earth is rotating, a full tidal cycle takes 50 minutes longer than the 24 hours it takes the earth to make a complete rotation.

When the sun and moon are at right angles their effects partially cancel each other. During these **neap tides** the tidal range is small. Neap tides occur when the moon is in the first and third quarters.

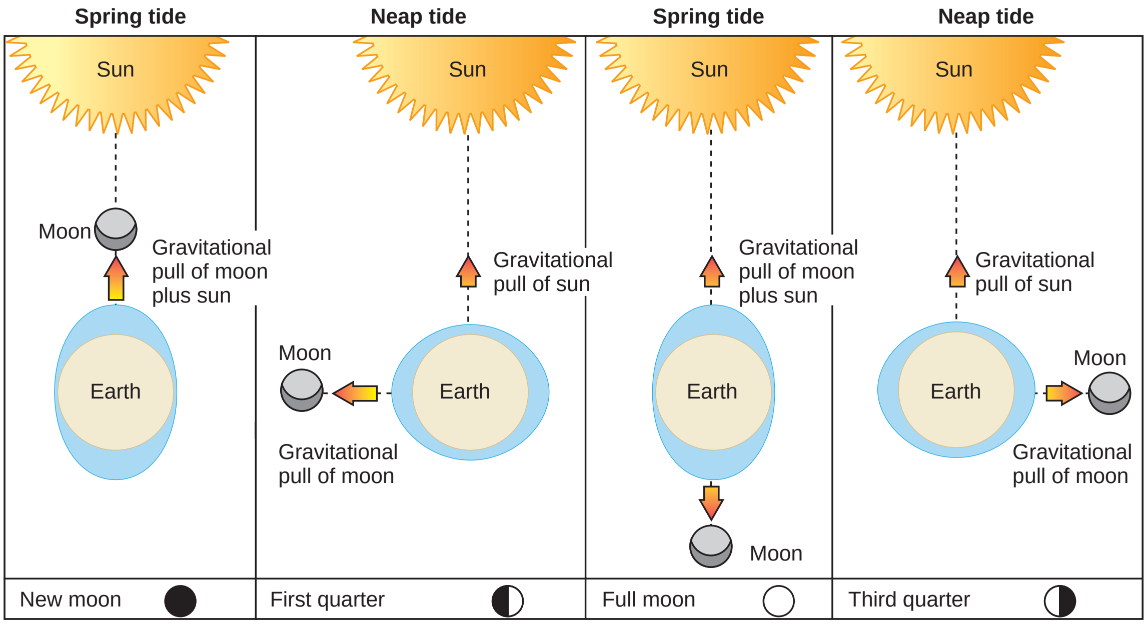

Spring tide
Neap tide
Spring tide
Neap tide
Sun
Sun
Sun
Sun
Moon
Gravitational pull of moon plus sun
Earth
Gravitational pull of sun
Moon
Earth
Gravitational pull of moon
Gravitational pull of moon plus sun
Earth
Moon
Gravitational pull of sun
Moon
Earth
Gravitational pull of moon
New moon ●
First quarter ◐
Full moon ○
Third quarter ◑

FIGURE 3.33 The tidal bulges are largest, and therefore the tidal range is greatest, when the moon and sun are in line and acting together. This happens at new and full moon. When the moon and sun are pulling at right angles, which occurs when the moon is in quarter, the bulges and tidal range are smallest.

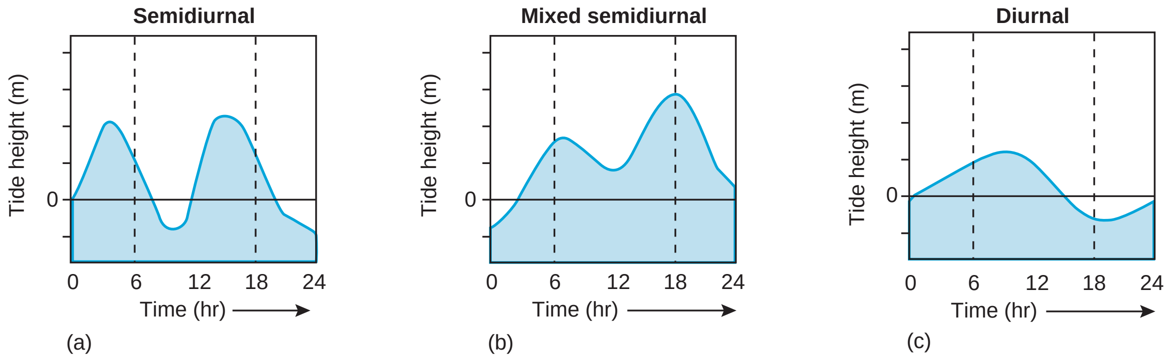


FIGURE 3.34 Types of tides. In most places the tide is semidiurnal; that is, there are two high and two low tides per day. (*a*) In some places, successive high tides are nearly equal in height. (*b*) In many other places, one of the high tides is considerably higher than the other. This is called a mixed semidiurnal tide. (*c*) A few places have a diurnal tide, with only one high and one low tide per day.

> The tides are caused by a combination of the gravity of the sun and moon and the centrifugal force that results from the rotation of the earth, moon, and sun.

Tides in the Real World Fortunately for us, the earth is not completely covered with water. Largely because of the continents and the shape of the sea floor, tides in the real world behave somewhat differently than they would on a water-covered earth. As predicted, most places do have **semidiurnal tides,** which means there are two high tides and two low tides a day (Fig. 3.34*a* and *b*). The east coast of North America and most of Europe and Africa have semidiurnal tides (Fig. 3.35). Some places have a **mixed semidiurnal tide,** with successive high tides of different height (Fig. 3.34*b*). Mixed semidiurnal tides are characteristic of most of the west coast of the United States and Canada. **Diurnal tides** occur when there is only one high and one low tide every day (Fig. 3.34*c*). Diurnal tides are uncommon. They occur on the coast of Antarctica and in parts of the Gulf of Mexico, Caribbean, and Pacific (Fig. 3.35). The distinctions between the types of tide illustrated in Figure 3.34 are not absolute, and in most places the tidal pattern varies somewhat. Southern California, for example, has a predominantly mixed semidiurnal tide but sometimes the tides are almost diurnal.

Tides vary from place to place and time to time because of the effects of continents, islands, and bottom topography. On a water-covered earth with a perfectly flat sea floor, the tides would

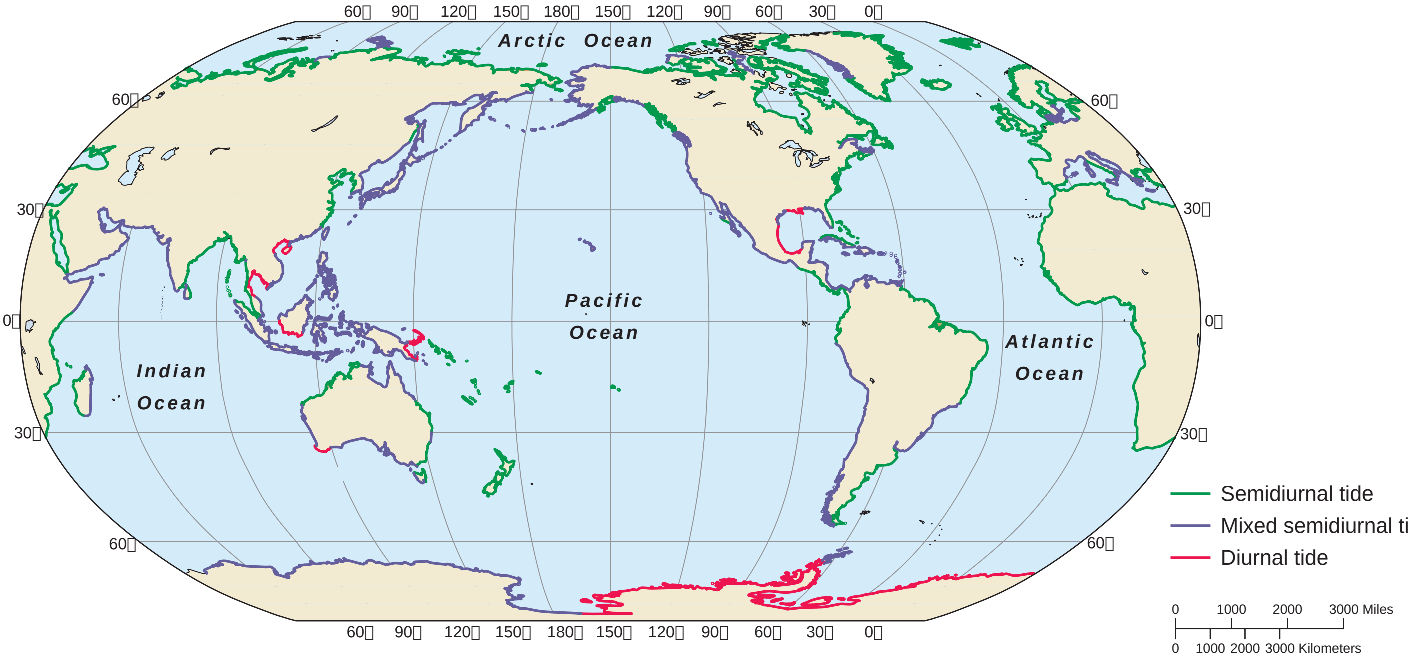


FIGURE 3.35 The worldwide distribution of semidiurnal, mixed semidiurnal, and diurnal tides. This map shows the dominant type of tide. At most places there is variation; a place that usually has, say, a mixed semidiurnal tide may occasionally experience diurnal tides.

move around the earth in a smooth, symmetrical wave. In the real world, however, the continents prevent the wave from sweeping around the globe, essentially breaking the wave into several separate waves within individual basins. Islands, ridges, basins, canyons, reefs, and other features further affect the waves. The tide at a given place thus depends on its location relative to these features. The tides are also influenced by variation in the orbits of the sun and moon relative to the Equator, and the planets have small effects. Even the weather can affect the tides. Strong winds, for example, can pile water up on shore, causing higher tides than would otherwise occur. To predict the tides at a given place, oceanographers have to combine observations of actual tides at that place with their theoretical equations. They are then able to produce remarkably accurate **tide tables** that predict the time and height of high and low tides. Tide tables are available for most coastal areas.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. In unusually cold winters the northern Black Sea sometimes freezes, while the nearby Adriatic Sea usually doesn't, even if it is just as cold. Freshwater runoff gives the surface of the Black Sea a low salinity of about 18‰. What would you guess about the salinity of the Adriatic?
2. Just for the fun of it, someone in Beaufort, South Carolina, throws a message in a bottle into the sea. Some time later, someone in Perth, on the west coast of Australia, finds the bottle. Referring to Figure 3.20 and the fold-out map at the back of this book, can you trace the path the bottle probably took?
3. If you owned a seaside home and a bad storm brought heavy winds and high surf to your coastline, would you prefer it to be during a new moon or a quarter moon? Why?
4. Most tsunamis occur in the Pacific Ocean, as indicated by the map in the "Waves That Kill" boxed reading (see p. 58). How would you explain this?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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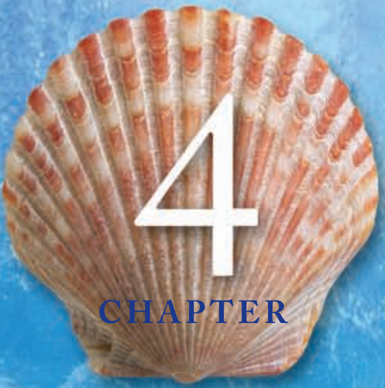


4 CHAPTER

Fundamentals of Biology

A shark (*Squalus acanthias*) embryo begins a new turn of the cycle of life.

Now that we have discussed some of the major features of the marine environment, we can turn our attention to life in the sea. Perhaps the most basic question we could ask is, What *is* life? Most people have a pretty good feel for what the word *living* means, but biologists have never agreed on a precise definition. About the best we can do is to describe the properties that living things have in common.

All living things use **energy,** the ability to do work, to maintain themselves and grow. This is accomplished by means of a vast number of chemical reactions that together are called **metabolism.** Living things also use energy to maintain stable internal conditions that are different from their surroundings, a process known as **homeostasis.** They are able to sense and react to the external environment. In addition, all life forms reproduce to perpetuate their kind and pass their characteristics on to their offspring.

All living things grow, metabolize, regulate their internal environment, react to the external environment, and reproduce.

The most basic features of living things are shared by all organisms, not just those that live in the sea. Here, however, we will pay particular attention to the lives of marine organisms.

THE INGREDIENTS OF LIFE

The process of life involves an intricate series of interactions among an immense variety of chemicals. The most important of these chemicals is also one of the simplest: **water.** As the universal solvent, water provides the medium in which all the other **molecules** dissolve and interact. Water is the base of a complex "chemical soup" inside all organisms where the chemical reactions of metabolism take place.

The Building Blocks

Besides water, most of the chemicals that make life possible are **organic compounds,** molecules that contain atoms of **carbon, hydrogen,** and usually **oxygen.** Organic compounds are high-energy molecules; that is, it takes energy to make them (Fig. 4.1). The ability to use energy to make, or synthesize, organic compounds is an important characteristic of living things. Organic compounds tend to break down when left to themselves. When this happens they release the energy that went into their construction. Organisms have developed the ability to control this breakdown, often in order to harness the energy that is released.

Carbohydrates Most organic molecules belong to one of four main groups. **Carbohydrates** are composed mainly of just the basic elements of other organic molecules: carbon, hydrogen, and oxygen. The simplest carbohydrates are **glucose** and a few other **simple sugars.** More complex carbohydrates are formed by the combination of simple sugars into chains. Ordinary table sugar, for example, consists of two simple sugar molecules joined together. **Starches** and other complex carbohydrates consist of much longer chains, which may contain components other than simple sugars.

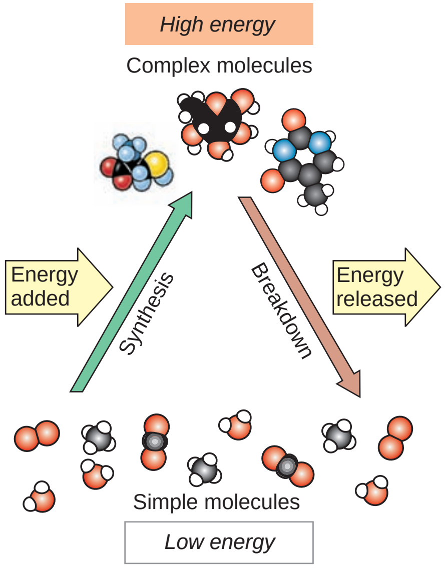
Organisms use carbohydrates in many ways. Simple sugars play a vital role in the most basic metabolic processes, as we shall see. Complex carbohydrates like starches are often used to store energy reserves.

Some carbohydrates are **structural molecules,** which provide support and protection. For example, some animals use **chitin,** a modified carbohydrate, as a skeletal material. Plants and many algae produce a structural carbohydrate called **cellulose,** the main ingredient of wood and plant fibers (see Table 6.1, p. 113). Other carbohydrates have roles in reproduction, metabolism, and interactions among cells—in fact, in nearly every biological function—that scientists are only beginning to understand.

Proteins **Proteins** are another major group of organic molecules. Like complex carbohydrates, proteins are composed of chains of smaller subunits. In proteins the subunits are **amino acids,** which contain atoms of **nitrogen** as well as the carbon, hydrogen, and oxygen typical of all organic compounds.

Proteins have an extraordinary variety of functions. Muscles are made largely of protein. **Enzymes** are proteins that speed up, or catalyze, specific chemical reactions. Without enzymes, most metabolic reactions would proceed very slowly or not at all. There are also many structural proteins, including those in the skin, hair, and skeletons of some marine animals. Some **hormones,** chemicals that act as messengers to help different parts of the body work together, are proteins. Other proteins carry oxygen in the blood and muscles. Proteins also act as poisons, send chemical signals, produce light, act as antifreeze in the blood of some Antarctic fishes, and have countless other functions.

FIGURE 4.1 Chemical reactions can be divided into those that require energy and those that release it. Organisms need energy to make complex molecules from simple ones, much as energy is required to push a rock uphill. The breakdown of energy-rich complex molecules is a "downhill" process that releases energy.



Lipids Fats, oils, and waxes are examples of **lipids,** another group of organic chemicals. Lipids are often used for energy storage (Fig. 4.2). Another useful property of lipids is that they repel water. Many marine mammals and birds, for instance, use a coating of oil to keep their fur or feathers dry. Some marine organisms that are exposed to the air at low tide have a coating of wax that helps keep them from drying out. Lipids are also useful in buoyancy because they float, and as insulation from the cold. Some hormones are lipids rather than proteins.

Nucleic Acids **Nucleic acids** store and transmit the basic genetic information of all living things. Nucleic acid molecules are chains of repeating subunits called **nucleotides** that consist of a simple sugar joined to molecules containing phosphorus and nitrogen. The nitrogen-containing molecule is called the **nitrogen base** of the nucleotide. One type of nucleic acid is **DNA (deoxyribonucleic acid).** An organism's DNA molecules specify the "recipe" for the organism—all the instructions for its construction and maintenance. An organism's complete genetic information is called its **genome.** The organism inherits this genetic information, in the form of DNA, from its parents and passes it on to its offspring. The DNA chains are often tens or hundreds of millions of nucleotides long, but the nucleotides contain only four different types of nitrogen bases: adenine, cytosine, thymine, and guanine. The order, or **sequence,** of the different nucleotides on the chain forms a code, like a four-letter alphabet, that contains the genetic information. Four letters may not sound like much, but Morse code can express any written message using only two "letters": dots and dashes. DNA's "words" are **genes,** sequences of DNA that specify the order of amino acids in a single protein.

Water is called the **universal solvent** because it can dissolve more different substances than any other liquid.

- Chapter 3, p. 43

Molecules Combinations of two or more *atoms;* most substances are composed of molecules rather than individual atoms.

- Chapter 3, p. 41

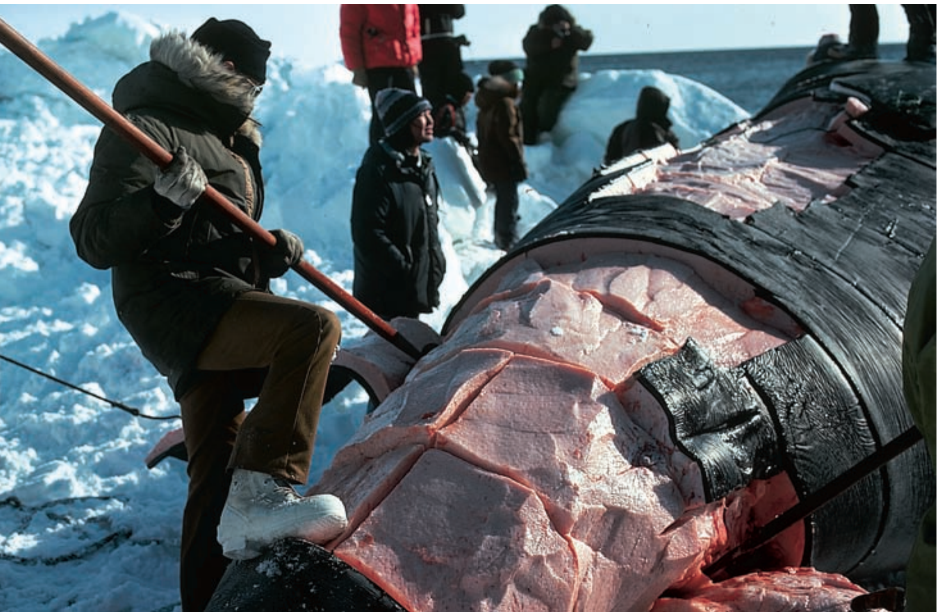


FIGURE 4.2 The thick layers of blubber on this whale are composed almost entirely of lipid. Whales can go without eating for long periods by using the energy stored in the blubber. The whale's blubber also helps protect it from the cold and gives it buoyancy. People once used the energy contained in blubber by burning oil made from it for light and heat. Most industrial whaling has ceased but so-called traditional whaling, such as that undertaken by these Alaskan Inuit, continues legally in some places.

Another group of nucleic acids is **RNA (ribonucleic acid).** Like DNA, RNA consists of chains of only four types of nucleotides. Three of these are the same as in DNA, but the fourth kind of nucleotide in RNA contains uracil instead of thymine. Many RNA molecules help convert the genetic information encoded in DNA into proteins. Some RNAs catalyze chemical reactions much as enzymes do. Biologists have recently discovered other RNAs with a range of previously unknown functions including storing genetic information in their own right, helping control whether genes in DNA are translated into proteins, and helping fight viral infections.

Because organisms' nucleic acids define so much about them, sequencing nucleic acids—determining their nucleotide sequences—has become one of the hottest fields of biological research. Complete genome sequences are known for only a small but increasing number of organisms, most notably humans. Partial nucleic acid sequences are available for many more organisms and contain a wealth of information. These sequences can be used as genetic "bar codes" to identify species, including ones that have never been collected, and shed light on details of their metabolism and lifestyle (see "Tiny Cells, Big Surprises," p. 92, and "The Census of Marine Life," p. 216).

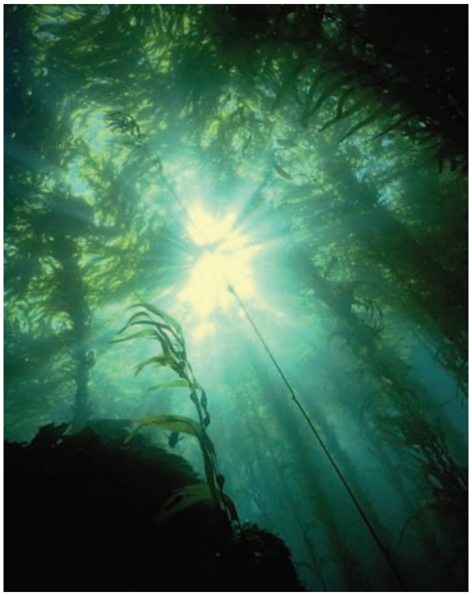


FIGURE 4.3 Giant kelp (*Macrocystis*), a seaweed from the temperate Pacific Ocean, captures the sunlight streaming down through the water to perform photosynthesis. The kelp uses the light energy to grow. Other organisms eat the kelp, making use of the energy that originally came from the sun.

Organic compounds are chemicals that contain carbon, hydrogen, and usually oxygen. The main types of organic compounds are carbohydrates, proteins, lipids, and nucleic acids.

The Fuel of Life

The molecules that make up living things interact in many complex chemical systems. The most basic of these have to do with the capture, storage, and use of energy or, more simply put, with the production and use of food. These systems store and transfer energy using **ATP (adenosine triphosphate)** as a common "energy currency." ATP is a high-energy molecule based on adenosine, one of the nucleotides in nucleic acids. Energy is stored as chemical energy by converting a related but lower-energy molecule, **ADP (adenosine diphosphate),** into ATP. When the ATP is broken back down into ADP the energy is transferred to other molecules to be used in metabolism. In an average day a person cycles through 57 kg (125 lb) of ATP. Whales must use tons!

Organisms transfer energy between different molecules using ATP (adenosine triphosphate), the energy currency of life.

Microorganisms use a variety of metabolic pathways to process energy (see Table 5.1, p. 88). Most other organisms, however, largely rely on only two: photosynthesis and respiration.

Photosynthesis: Making the Fuel

Most organisms ultimately get their energy from the sun (Fig. 4.3). In **photosynthesis,** algae, plants, and some other organisms capture the sun's energy and use it to make glucose, a simple sugar, some of which is converted into other organic compounds. Most other organisms use these organic molecules as a source of energy. Organic material contains a tremendous amount of energy. As food it fuels our bodies and those of most other creatures. In such forms as oil, gas, and coal, it heats our homes, runs our factories, and powers our cars.

Photosynthesis (Fig. 4.4) begins when solar energy, in the form of sunlight, is absorbed by chemicals within an organism called **photosynthetic pigments.** The most common photosynthetic pigment is **chlorophyll,** which gives plants their characteristic green color. Most algae have additional pigments that often mask the green

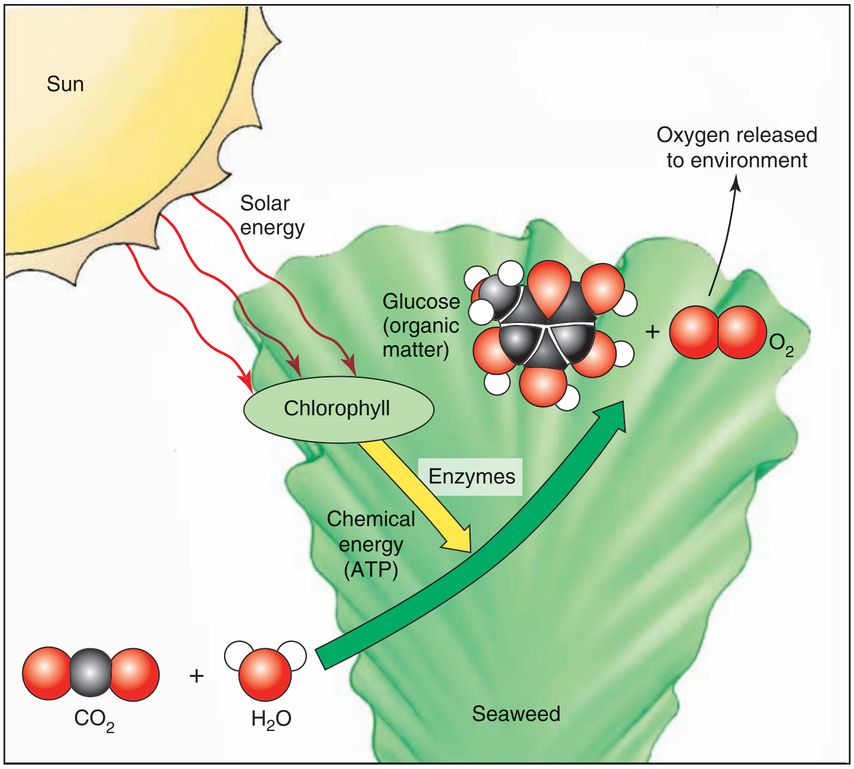


FIGURE 4.4 In photosynthesis, carbon dioxide and water are used to make glucose. The energy for this process comes from sunlight. Oxygen is given off as a by-product.

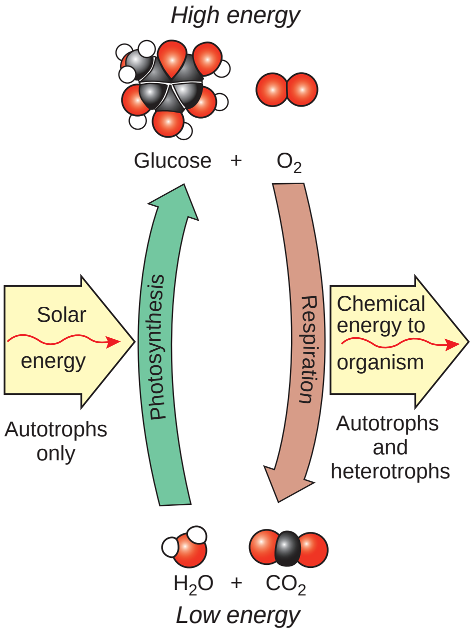


FIGURE 4.5 Respiration is basically the opposite of photosynthesis. Respiration breaks down glucose, using oxygen, and produces carbon dioxide and water. The energy that originally came from the sun is then made available to the organism.

chlorophyll (see Table 6.1, p. 113). Because of these pigments, algae may be brown, red, or even black instead of green.

In a long series of enzyme-controlled reactions, the solar energy captured by chlorophyll and other pigments is converted into chemical energy, in the form of ATP, and then used to make glucose, with **carbon dioxide** (CO_2) and water (H_2O) as the raw materials. Carbon dioxide is one of very few carbon-containing molecules not considered to be an organic compound. Photosynthesis, then, converts carbon from an inorganic to an organic form. This is called **fixing** the carbon, or **carbon fixation.** The solar energy absorbed by chlorophyll is stored as chemical energy in the form of glucose. The glucose is then used to make other organic compounds (see "Primary Production," p. 68). ATP may be the "energy currency" of the cell, but fixed carbon—organic matter—is the "currency" in which energy flows through food webs and ecosystems.

In addition to fixing carbon, photosynthesis produces **oxygen gas** (O_2), as a by-product. All the oxygen gas on earth, both in the atmosphere we breathe and in the ocean, was produced by photosynthetic organisms, which constantly replenish the earth's oxygen supply. Thus, we rely on photosynthesis not only for food, but for the very air we breathe.

Photosynthesis captures light energy from the sun to produce glucose. Carbon dioxide and water are used to make the glucose, and oxygen gas is liberated as a by-product:

$$H_2O + CO_2 \xrightarrow{\text{sun energy}} \underset{\text{(glucose)}}{\text{organic matter}} + O_2$$

Organisms that are capable of photosynthesis can obtain all the energy they need from sunlight and do not need to eat. Such organisms are called **autotrophs** ("self-feeders"). Plants are the most familiar autotrophs on land. In the ocean, however, bacteria and algae are the most important autotrophs.

Many organisms cannot produce their own food and must obtain energy from organic matter that already exists. These organisms, which include all animals, are called **heterotrophs.**

Respiration: Burning the Fuel Both autotrophs and heterotrophs perform **respiration** to make use of the solar energy stored in organic chemicals by photosynthesis. Though the chemical reactions are different, the net result of oxygen-dependent, or **aerobic,** respiration is essentially the reverse of photosynthesis (Fig. 4.5). Sugars are broken down using oxygen, and carbon dioxide and water are given off. This process is sometimes called cellular respiration to distinguish it from the physical act of breathing. Since breathing acts to provide oxygen for cellular respiration, the two processes are related.

Respiration, which occurs in nearly all organisms, breaks down glucose, releasing the energy it contains. Respiration consumes oxygen and produces carbon dioxide and water:

$$\underset{\text{(glucose)}}{\text{organic matter}} + O_2 \xrightarrow[\text{chemical energy}]{} CO_2 + H_2O$$

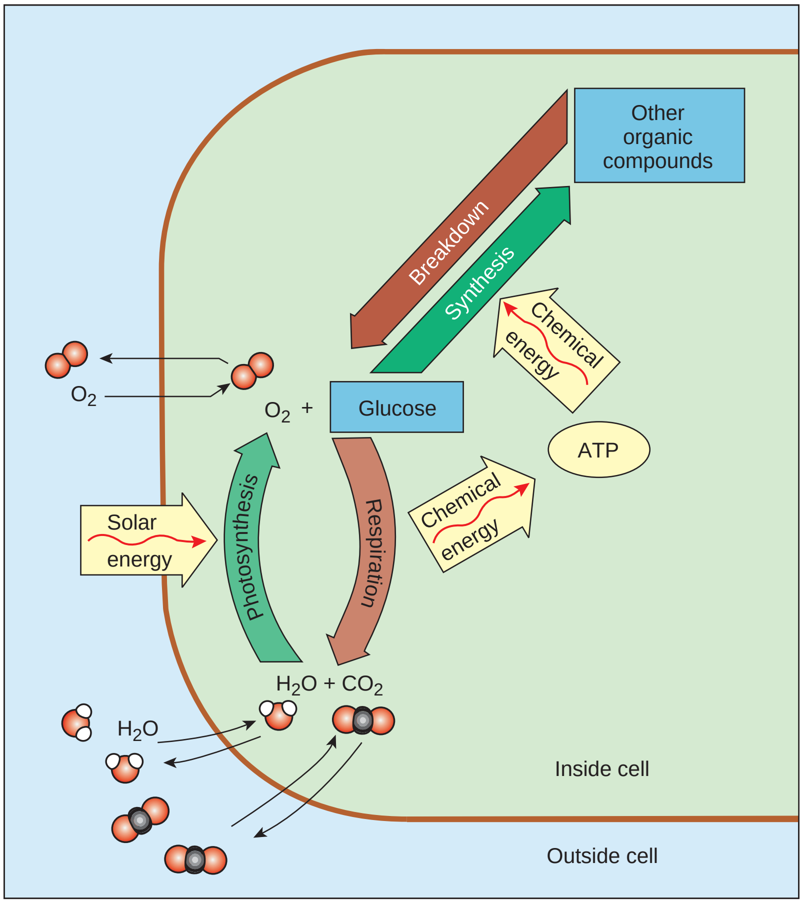


FIGURE 4.6 In photosynthesis, autotrophs capture energy from the sun and store it as chemical energy in simple sugars like glucose. Some of the sugars are broken down in respiration, and the energy is stored in ATP. This makes the energy available to the rest of the organism's metabolism—for example, to make other organic matter from the remaining glucose. If there is no light, autotrophs can perform only respiration, like animals and other heterotrophs. The thin black arrows represent molecules moving in and out of the cell.

Respiration is similar to the burning of wood or oil in that organic material is broken down, oxygen is consumed, and the energy contained in the material is released. That is why dieters speak of "burning calories." In respiration, however, the energy stored in the organic material is not released in flames. Instead, it is stored in ATP.

If oxygen is not available many organisms are able to use a different form of respiration called **anaerobic** respiration. Anaerobic respiration does not require oxygen, but it is not as efficient as aerobic respiration and provides less energy to the organism. Many animals, however, temporarily switch to anaerobic respiration when extreme exertion depletes the oxygen in their muscles and blood. Some organisms that live in oxygen-depleted environments, such as muddy sediments or the guts of fishes, use anaerobic respiration all the time. Aerobic respiration is more widespread than anaerobic respiration, however, and in this text the general term "respiration" refers to aerobic, or oxygen-dependent, respiration.

Primary Production The sugars produced by photosynthesis supply both raw material and energy, via respiration, for the manufacture of other organic compounds. Through elaborate chemical processes, some of the glucose formed during photosynthesis is converted into other types of organic molecules—carbohydrates, proteins, lipids, and nucleic acids (Fig. 4.6). The energy for these conversions, in the form of ATP, comes from "burning up," or metabolizing, much of the rest of the glucose. Thus, most of the glucose produced by photosynthesis is either converted to other types of organic matter or respired to fuel this conversion.

When autotrophs produce more organic matter than they use in respiration, there is a net increase in organic matter, which is called **primary production.** The autotrophs use the extra organic material to grow and reproduce. In other words, the extra organic matter forms more living material, and that means more food for animals and other heterotrophs. Organisms that perform this primary production of food are called **primary producers,** or sometimes just **producers.**

Primary production is the net gain in organic matter that occurs when autotrophs make more organic matter than they respire, usually by photosynthesis.

The Importance of Nutrients Only carbon dioxide, water, and sunlight are needed to make glucose by photosynthesis, but additional materials are needed to convert the glucose into other organic compounds. These raw materials, called **nutrients,** include minerals, vitamins, and other substances. Primary producers use large amounts of nitrogen, which is needed to make proteins, nucleic acids, and other compounds. **Nitrate (NO_3^{-1})** is the most important form of nitrogen in the ocean, though nitrogen is used in other forms (see "Cycles of Essential Nutrients," p. 226). Phosphorus, needed to make nucleic acids and other compounds, is another important nutrient. Its main source is **phosphate (PO_4^{-2}). Diatoms, radiolarians,** and **silicoflagellates** require large amounts of **silica (SiO_2)** to make their shells. Another important nutrient is **iron** in various forms. Although needed in much smaller amounts than nitrogen, phosphorus, or silica, iron is in critically short supply in large parts of the ocean (see "Nutrients," p. 346).

Primary production by photosynthesis requires nutrients as well as light. Nitrogen, phosphorus, silica, and iron are the most important nutrients in the ocean.

LIVING MACHINERY

The chemical reactions of metabolism make life possible, but chemical reactions are not living things and organisms are not just bags of chemical soup. If you ran a fish, say, through a blender, you would have all the same molecules, but the fish would definitely not be alive. The molecules in living things are *organized* into structural and functional units that work in a coordinated way. It is this living machinery that is responsible for many of the properties of living things.

Cells and Organelles

The basic structural unit of life is the **cell.** All organisms are made of one or more cells. Cells contain all the molecules needed for life packaged in a living wrapper called the **cell membrane,** or **plasma membrane.** This membrane isolates the gelatinous contents of the cell, or **cytoplasm,** from the outside world. The cell membrane allows some substances to pass in or out but prevents others from doing so.

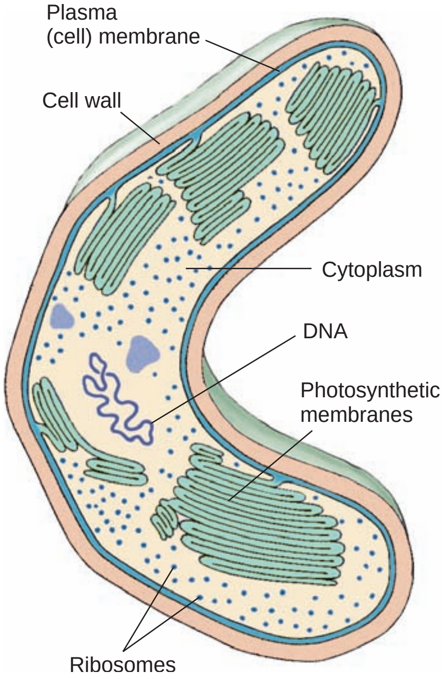
There are a number of structures within the cytoplasm. Among the most important are membranes similar to the outer cell membrane. These interior membranes act as sites for such chemical processes as photosynthesis and respiration. Membranes may also divide the cell into compartments that enclose still more complex structures specialized for particular tasks. These membrane-bound structures are known as **organelles.**

Cells also have a complex internal framework made of protein fibers. This framework, called the **cytoskeleton,** supports the cell, allows it to move and change shape, and helps it divide.

Structurally Simple Cells: Prokaryotes **Prokaryotic cells** are primitive in the sense that they are the most ancient of the two major types of cells. They are also the simplest and smallest cells. Prokaryotic cells are distinguished by the absence of most kinds of organelles (Fig. 4.7), though some prokaryotes do have certain organelles or organelle-like structures. Organisms with prokaryotic cells are called **prokaryotes.** With very few exceptions (see Fig. 5.3), prokaryotes are microscopic, and most are tiny even by the standards of microscopic organisms. **Bacteria** are the best-known group of prokaryotes.

Outside the cell membrane of prokaryotes lies a supportive **cell wall.** Inside, the cell has a single, ring-like molecule of DNA. Attached to the cell membrane and scattered through the cytoplasm are small structures made of protein and RNA called **ribosomes.** The cell's proteins are made in the ribosomes. In photosynthetic prokaryotes, folds of the plasma membrane contain photosynthetic pigments. Some prokaryotes have one or more protein filaments known as **flagella** (singular, **flagellum**) that extend outside the cell membrane. These cells move by rotating their flagella like tiny propellers.

FIGURE 4.7
Prokaryotic cells have a plasma membrane lying inside a cell wall. The plasma membrane is where respiration occurs and may fold into the cell's interior. Membrane folding is particularly pronounced in photosynthetic bacteria like this one. The folds contain chlorophyll and are the site of photosynthesis. Prokaryotic cells also contain scattered ribosomes and a ring-like molecule of DNA. Otherwise there is relatively little structure inside the cell.



The most primitive cells are prokaryotic. They have relatively little internal structure and lack most kinds of membrane-bound organelles.

Structurally Complex Cells: Eukaryotes **Eukaryotic cells,** the second major cell type, are more organized and complex than prokaryotic cells (Fig. 4.8). Various membrane-bound organelles found only in **eukaryotes** do specialized jobs within the cell. The **nucleus** contains **chromosomes** that carry most of the cell's DNA. The nucleus thus holds the cell's genetic information and directs most of its activities. The nucleus can be thought of as the cell's headquarters.

The "factories" of eukaryotic cells are two structures, mostly folded membranes, called the **endoplasmic reticulum** and the **Golgi apparatus.** These organelles make, package, and transport many of the organic molecules that the cell needs. Ribosomes sit in some of the endoplasmic reticulum.

Respiration in eukaryotes takes place in special organelles called **mitochondria.** Mitochondria are the cell's power plants, breaking down organic molecules to provide energy. Plant and algal cells have two important structures that animals don't. First, they have **chloroplasts,** chlorophyll-containing organelles where photosynthesis takes place. Second, except for some single-celled algae, they have a cell wall.

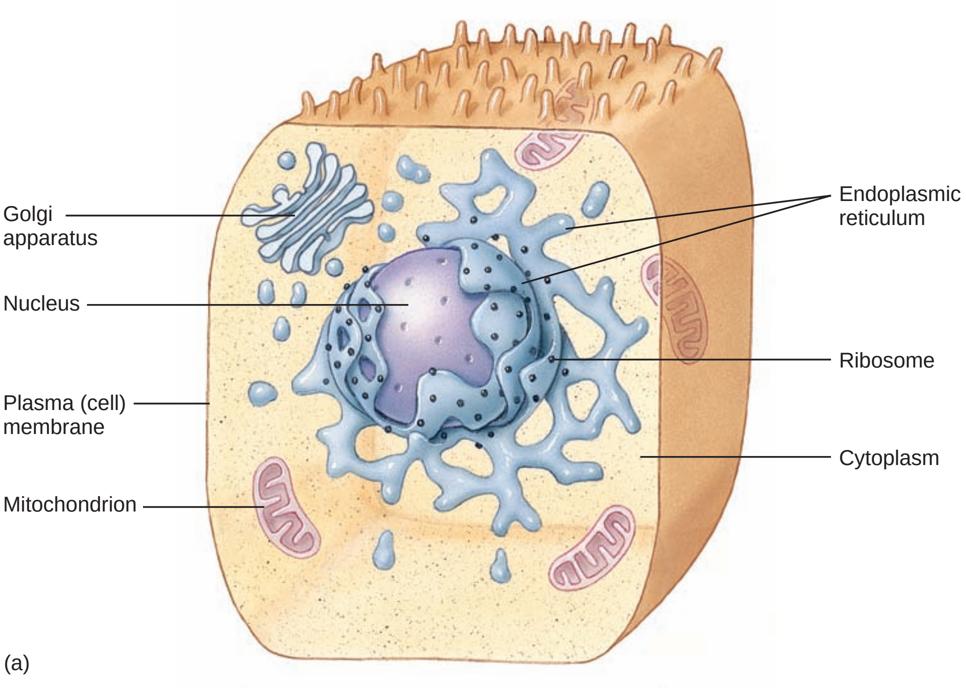
Eukaryotic cells often have flagella, which are called **cilia** when they are short and numerous. Eukaryotic flagella and cilia differ from prokaryotic flagella in being enclosed in a membrane and having a more complex structure. Eukaryotes often swim with their flagella or cilia, but eukaryotic flagella beat back and forth instead of rotating like prokaryotic flagella. Eukaryotes also often use cilia and flagella to push water or particles through or over their bodies, rather than to push their bodies through the water. Many marine animals, for example, use cilia to push food particles to the mouth. Cilia in your lungs carry away dust and other irritants.

The cells of eukaryotes are more structured than those of prokaryotes. They have membrane-bound organelles, including a nucleus in which the DNA is carried in chromosomes.

Diatoms Single-celled algae with a shell, or test, made of silica.
- Chapter 5, p. 94, Figure 5.6

Radiolarians Single-celled protozoans with a test made of silica.
- Chapter 5, p. 98, Figure 5.12

Silicoflagellates Single-celled algae with a skeleton made of silica.
- Chapter 5, p. 97, Figure 5.9



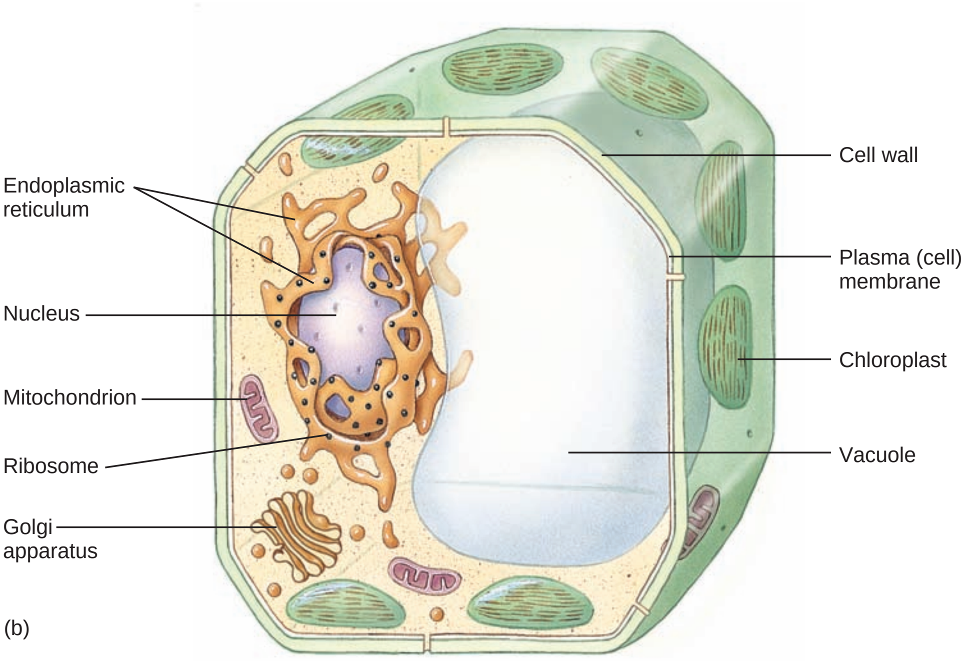


FIGURE 4.8 Typical cells of (*a*) animals and (*b*) algae and plants, and some of the structures they contain.

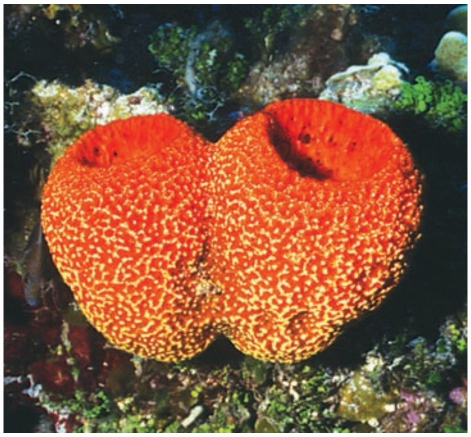


FIGURE 4.9 Sponges are the only multicellular animals that are at the cellular level of organization (see "Sponges," p. 116). Even sponges have specialized cells, though they don't form tissues.

Levels of Organization

A cell is a self-contained unit that can carry out all the functions necessary for life. Indeed, many organisms get by just fine with only a single cell. One-celled organisms are called **unicellular.** All prokaryotes and some eukaryotes are unicellular. Most eukaryotic organisms, however, are **multicellular;** that is, they have more than one cell. The human body, for instance, contains something like 100 trillion cells.

There is a division of labor among the cells of multicellular organisms, with different cells becoming specialized for particular jobs. Groups of specialized cells that perform the same task may be organized into more complex structures. The extent of this specialization and organization is referred to as the **level of organization** (Table 4.1).

At the **cellular** level of organization, each cell is essentially an independent, self-sufficient unit. Each can perform all the functions needed to sustain the organism and reproduce, and there is little or no cooperation among the cells.

Only a few multicellular organisms remain at the cellular level (Fig. 4.9). In most, certain groups of cells act together to do a particular job. These specialized, coordinated groups of cells are called **tissues.** Some cells, for example, are specialized to contract and do work. These cells are bound together to form muscle tissue. Nervous tissue, specialized to collect, process, and transmit information, is another example.

In most animals organization doesn't stop at the tissue level, either. Their tissues are further organized into structures known as **organs** that carry out specific functions. The heart is an example of an organ. There are several different tissues that make up the heart. Muscle tissue, for example, allows the heart to contract and pump blood, and nervous tissue controls the muscle.

Different organs act together in **organ systems.** The digestive system, for instance, includes many organs: mouth, stomach, intestine, and so on. Animals usually have a number of organ systems, including nervous, digestive, circulatory, and reproductive systems.

Table 4.1 Levels of Organization of Biological Systems

Increasing complexity

Level	Description	Examples	
Ecosystem	A community or communities in a large area, together with their physical environment	Nearshore ecosystem	One or more organisms
Community	All the populations in a particular habitat	Rocky shore community	
Population	A group of organisms of the same species that occur together	All the mussels on a stretch of rocky shore	
Individual	A single organism	One mussel	
Organ system	A group of organs that work in cooperation	Digestive system	Within individual organisms
Organ	Tissues organized into structures	Stomach	
Tissue	Groups of cells bound together and specialized for the same function	Muscle tissue	
Cell	Independent cells, the fundamental unit of living things	Muscle cell, single-celled organisms	
Organelle	A complex structure within cells, bound by a membrane	Nucleus, mitochondrion	Within cells
Molecule	Combinations of atoms that are bound together	Water, proteins	
Atom	The fundamental unit of all matter	Carbon, phosphorus	

Complex organization also exists at levels above that of the individual organism. A **population** is a group of organisms of the same kind, or **species,** that lives in one place. The mussels on a stretch of rocky shore, for example, form a population (Fig. 4.10).

Populations of different species that occur in the same place form **communities.** A community is more than just a collection of organisms that happen to live in the same area. The characteristics of communities are determined in large part by the way the organisms *interact*—which organisms eat each other, which compete, and which depend on each other (see "Ways That Species Interact," p. 213). Rocky shores, for example, are home to many organisms in addition to mussels: seaweeds, crabs, barnacles, snails, and sea stars, to name a few (Fig. 4.11). It is the interactions among all these organisms that give the rocky shore community its own unique structure.

A community, or often several communities, together with the physical, or non-living, environment, make up an **ecosystem.** The rocky shore community, for instance, along with other nearby communities, is part of a larger ecosystem that includes the tides, currents, nutrients dissolved in the water, and other physical and chemical aspects of the area.

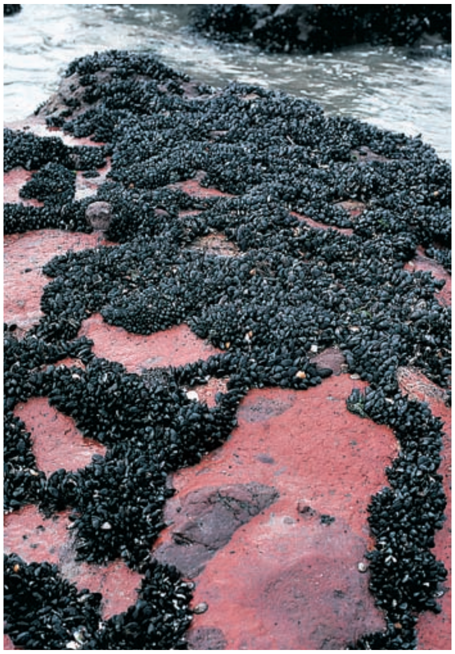


FIGURE 4.10 These blue mussels (*Mytilus edulis*) growing on a rocky shore in New Zealand are part of a population.

CHALLENGES OF LIFE IN THE SEA

Every **habitat** has its own unique set of characteristics and presents special challenges to the organisms that live there. Thus, marine organisms must cope with problems unlike those of land dwellers. Even within the marine environment there are different habitats, each of which poses special difficulties. For example, **planktonic** organisms—those that drift in the water—face very different conditions than **benthic** organisms—those that live on the bottom—or **nekton**—organisms that are strong swimmers (see Fig. 10.11). Organisms have evolved innumerable ways to adapt to the conditions of their habitats.

Many of the adaptations of marine organisms have to do with maintaining homeostasis. The living machinery inside most organisms is rather sensitive and can operate properly only within a narrow range of conditions. Living things have therefore devised ways to keep their internal environments within this range regardless of the external conditions.

Habitat The natural environment where an organism lives.
- Chapter 2, p. 19

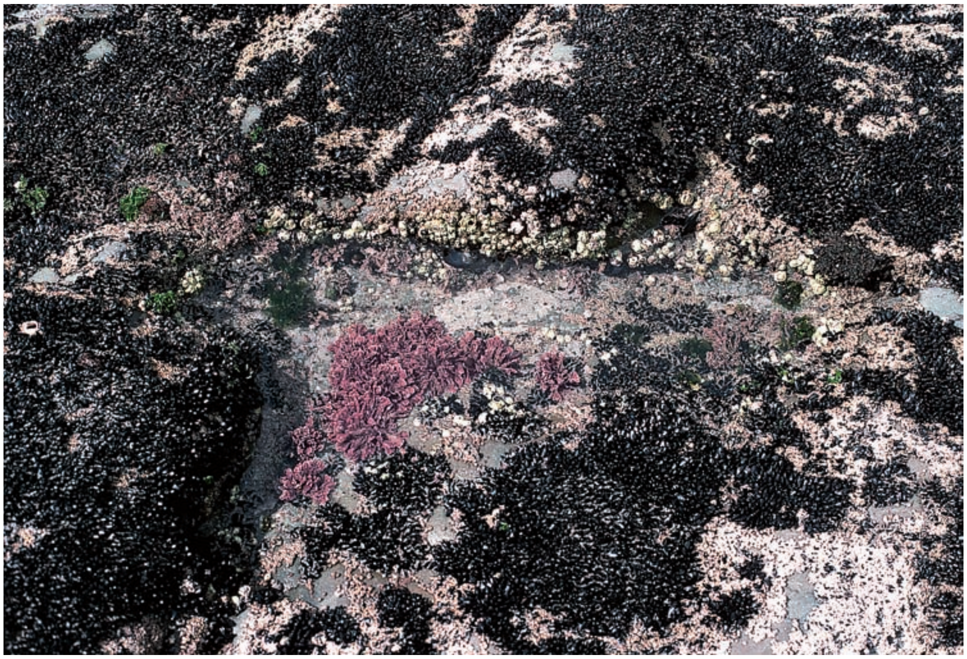


FIGURE 4.11 The community that lives on this rocky shore is made up of populations of blue mussels, barnacles, seaweeds, and many other species.

Salinity

Many enzymes and other organic molecules are very sensitive to the concentrations of **ions** in the cytoplasm. Marine organisms are immersed in a medium—seawater—that has the potential to profoundly alter their metabolism. To fully understand the problems posed by **salinity,** we must know something about how dissolved ions and molecules behave.

Diffusion and Osmosis When in solution, ions and molecules move around just like water molecules do. If the molecules are concentrated in one part of the solution, this random movement spreads them out until they are evenly distributed (Fig. 4.12). The overall result is that the molecules move from areas of high concentration to areas of low concentration. This process is called **diffusion.**

Whenever the internal composition of a cell differs from that on the outside, substances tend to move in or out of the cell by diffusion. If the surrounding seawater contains more sodium, say, than the cell's interior, sodium tends to diffuse into the cell. If the organism is sensitive to sodium, this presents a problem. Similarly, substances that are concentrated inside cells tend to diffuse out. Many of the cell's precious molecules—like ATP, amino acids, and nutrients—are much more concentrated in the cell than in seawater. Therefore, they tend to leak out of the cell.

One answer to this problem is to have some kind of barrier that prevents materials from diffusing in and out. The cell membrane is just such a barrier. It blocks the passage of the common ions in seawater as well as many organic molecules. The membrane cannot be a complete barrier, however, because the cell needs to exchange many materials—like oxygen and carbon dioxide—with its surroundings. The cell membrane is **selectively permeable;** that is, it allows some substances to enter and leave the cell but prevents others from doing so. Water and other small molecules pass readily through the cell membrane, for example, whereas ATP and many proteins do not.

The selective permeability of the cell membrane solves the problem of diffusion of ions and organic molecules, but it creates a new problem. Like any other molecule, water will diffuse from areas where it is concentrated to areas of lower concentration. If the total concentration of ***solutes*** inside the cell is higher than that outside, the concentration of *water* will be lower. Because water molecules are free to cross the cell membrane, they will stream into the cell, causing it to swell (Fig. 4.13). On the other hand, the cell will tend to lose water and shrivel if the total salt concentration outside the cell is higher than that inside. The diffusion of water across a selectively permeable membrane is known as **osmosis.**

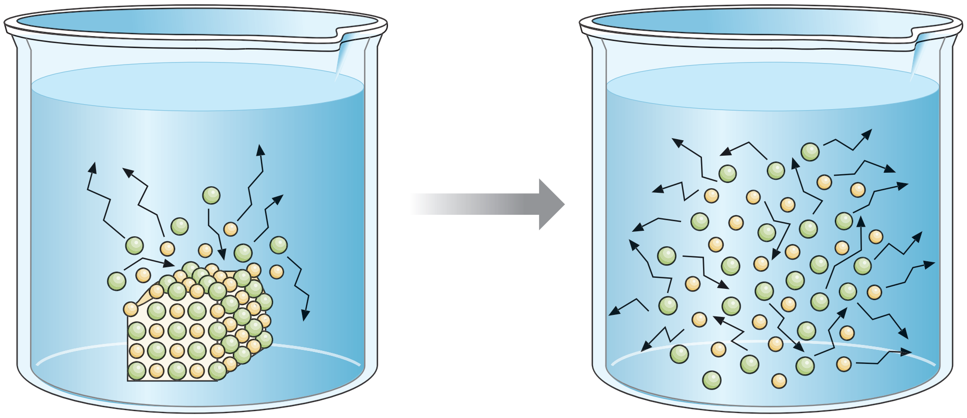


FIGURE 4.12 Ions and molecules dissolved in water tend to move around randomly just like water molecules do. When a crystal of salt dissolves in water, the ions start out concentrated in one part of the solution but eventually spread out because of their random movement. This process, called diffusion, results in the flow of ions from areas of high concentration to areas of low concentration.

Diffusion and osmosis always move materials from high concentration to low. The selective permeability of the cell membrane can control this movement, but not reverse it. Cells often need, however, to move materials in the opposite direction. They may, for example, need to rid themselves of excess sodium even though the seawater outside is more concentrated than the inside of the cell, or to take up sugars and amino acids from the surrounding water even though they are already more concentrated inside the cell. In the process of **active transport,** proteins in the cell membrane pump materials in the opposite direction to which they would move by diffusion. This process requires energy, in the form of ATP.

EVOLUTIONARY PERSPECTIVE

From Snack to Servant: How Complex Cells Arose

Prokaryotes were the first life on earth. There are fossil bacteria thought to be 3.8 *billion* years old, nearly as old as the oceans themselves. It was another billion years or more before eukaryotic cells appeared. Strangely enough, this advance in cell design, shared by all multicellular life, may have started with a simple "meal."

Biologists believe that mitochondria, the "powerhouses" of the cell (see Fig. 4.8), were once free-living bacteria. They are 1 to 3 microns (μm) long, about the same size as many bacteria. Respiration in both bacteria and mitochondria takes place in their membranes, and mitochondria have folded internal membranes similar to those found in many bacteria. Although most of a eukaryotic cell's DNA is contained in the nucleus, mitochondria have a small amount of their own DNA. This DNA is even in the form of a single, circular molecule like the chromosome of bacteria. When a cell needs new mitochondria, it does not make them from scratch. Instead, the mitochondria within the cell divide, much as bacteria reproduce by cell division. Mitochondria resemble bacteria in several other respects.

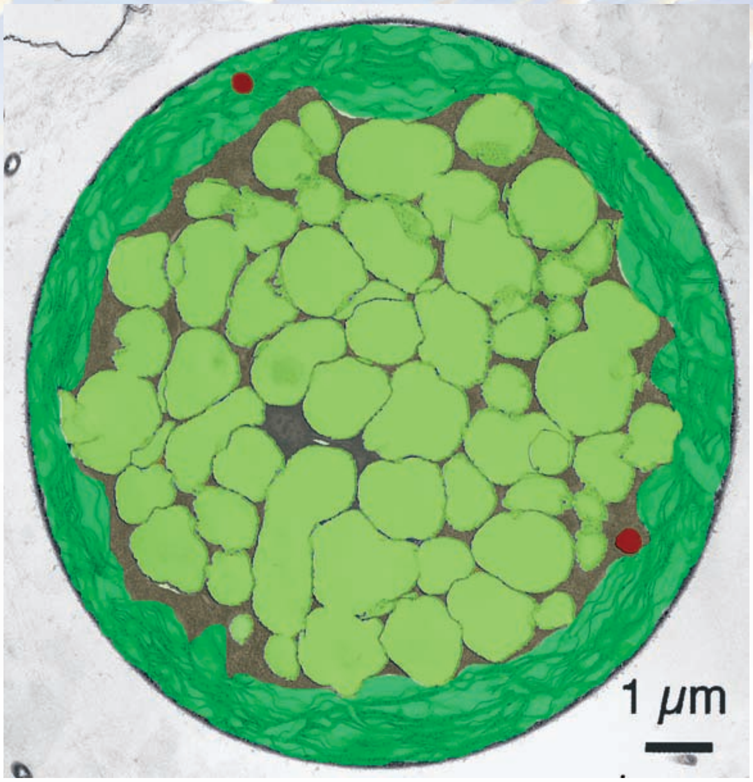
Because of these similarities, biologists believe that mitochondria were originally bacteria that came to live inside other cells. A relatively large cell that had already evolved some chemical features of today's eukaryotes may have engulfed a smaller one but been unable to digest it, or a disease-causing bacterium may have invaded the larger cell but not killed it. Both phenomena have been observed in the laboratory in living cells. Either way, the small cells eventually took up permanent residence in the larger cells, using them as hosts. The living together of different kinds of organisms like this is called **symbiosis** (see "Symbiosis," p. 218).

According to this theory, the host cells could not use oxygen in respiration. The smaller, symbiotic, bacteria did use oxygen and provided this ability to their hosts, giving them an advantage over cells without the symbionts.

Over time the host cells transferred most of the symbiotic bacteria's genes into their own nuclei, and thus came to control the symbionts. The symbionts and host cells became more and more dependent on each other. Eventually the symbionts became mitochondria.

Chloroplasts, the organelles that perform photosynthesis, are also thought to have arisen from symbiotic bacteria. Like mitochondria, they are about the right size, have a circular DNA molecule, and can reproduce themselves. Chloroplasts also contain folded membranes very similar to those of photosynthetic bacteria (see Fig. 4.7). Chloroplasts probably arose when a eukaryotic cell containing mitochondria engulfed a photosynthetic bacterium that wasn't digested and became symbiotic. The exact nature of this symbiont is hotly debated, but it probably looked something like a symbiotic bacterium called *Prochloron* that lives in some sea squirts and other invertebrates. The eukaryotic host cells gained the symbiont's photosynthetic ability and were the first algae. The algae eventually evolved different types of chloroplasts, which were later exchanged when one kind of alga engulfed another.

The hypothesis that mitochondria and chloroplasts arose from bacteria, once highly controversial, is now almost universally accepted by biologists. Some biologists even classify mitochondria and chloroplasts as symbiotic bacteria rather than organelles. All multicellular organisms, including humans, carry in their very cells the legacy of these bacterial partnerships, perhaps the result of an ancient snack.



Prochloron. This bacterium was once thought to be closely related to the symbiotic, photosynthetic bacterium that gave rise to chloroplasts, but genetic studies indicate that a slightly different group of bacteria was involved.

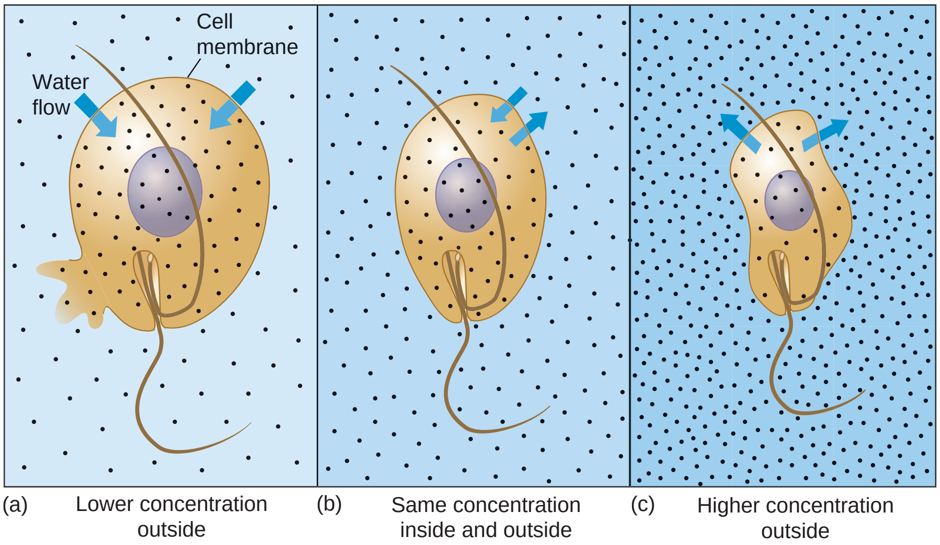
Active transport is so important that it represents over one-third of cells' total energy expenditure.

Diffusion is the movement of ions and molecules from areas of high concentration to areas of low concentration. Osmosis is the diffusion of water across a selectively permeable membrane. In active transport the cell uses energy to move materials in the opposite direction to diffusion.

Ions *Atoms* or groups of atoms that have a positive or negative charge. The most common ions in seawater are chloride and sodium.
- Chapter 3, p. 43

Solute Ions, organic molecules, or anything else that is dissolved in a solution.

Salinity The total amount of *salts* dissolved in water. Salts are combinations of ions.
- Chapter 3, p. 44



(a) Lower concentration outside (b) Same concentration inside and outside (c) Higher concentration outside

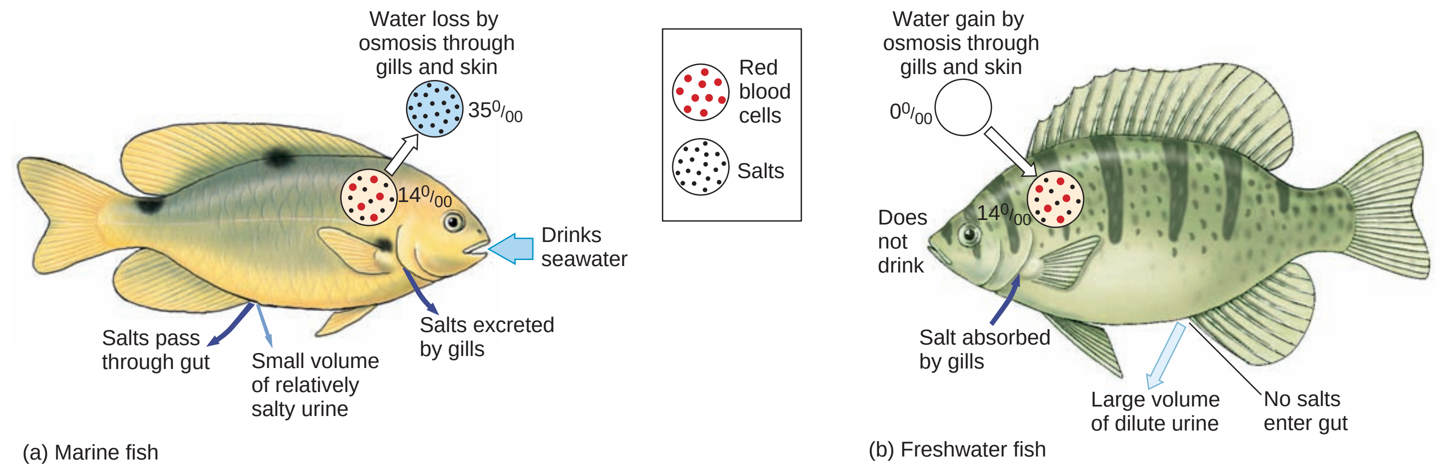
FIGURE 4.13 Osmosis. (*a*) If there is more dissolved material, and therefore less water, inside a cell than outside water will move into the cell by osmosis (a special case of diffusion). The cell will swell until it bursts. (*b*) If the internal and external concentrations are the same water moves in and out of the cell equally, and the cell stays in balance. (*c*) When the outside water is *more* concentrated, the cell loses water by osmosis and shrivels.

Regulation of Salt and Water Balance Marine organisms have adapted to the problems of maintaining the proper balance of water and salts in various ways. Actually, some do not actively maintain salt and water balance at all; their internal concentrations change as the salinity of the water changes (see Fig. 12.6). Such organisms are called **osmoconformers.** Many osmoconformers can live only in a narrow range of salinity. Others can tolerate relatively large changes in the salinity of the surrounding seawater (and therefore of their tissues), but even these osmoconformers have limits and experience osmotic problems outside their range of tolerance. In areas like the open ocean, where salinity doesn't fluctuate much, osmoconformers have few difficulties.

Other marine organisms **osmoregulate,** or control their internal concentrations to avoid osmotic problems. Osmoregulators still have limits, but are generally able to tolerate changes in salinity better than osmoconformers. One way osmoregulators adapt to different salinities is by adjusting the concentration of solutes in their body fluids so that the overall concentration of their fluids matches that of the water outside. It doesn't matter if there are the same dissolved chemicals inside and out as long as the total *amount* of dissolved material is the same. Therefore, some organisms osmoregulate by changing the amount of just one particular chemical to match changes in the salinity outside. Sharks, for example, increase or decrease the amount of a chemical called **urea** in their blood (see Fig. 8.18). A single-celled marine alga called *Dunaliella* uses a different chemical, glycerol, to do the same thing. *Dunaliella* may be the champion osmoregulator. It can maintain its water balance in water ranging from nearly fresh to more than nine times saltier than normal seawater.

By contrast, many osmoregulators maintain blood concentrations that are different from that of the surrounding seawater. Most marine fishes have body fluids considerably more dilute than seawater (Fig. 4.14*a*) and tend to lose water by osmosis. They replace the lost water by drinking seawater. They also conserve water by producing only a very small amount of urine. Some of the excess salts that are taken in with the seawater they drink are never absorbed and pass right through the gut. Marine fishes do absorb some of the salts they drink and must actively rid themselves of, or **excrete,** these excess salts. Some salts are excreted in the urine, but because so little urine is produced this is not enough. Most of the excess salts are excreted through the gills (see "Regulation of the Internal Environment," p. 164).

Freshwater fishes have the reverse problem: Their blood has a higher concentration of salt than the surrounding water, and they take in water by osmosis. Their adaptations are opposite those of marine fishes (Fig. 4.14*b*).



(a) Marine fish (b) Freshwater fish

FIGURE 4.14 Regulation of salt and water balance. (*a*) In most marine fishes, water flows by osmosis from the relatively dilute body fluids to the more concentrated seawater. To compensate and avoid dehydration, the fish drinks seawater. It excretes as little urine as possible to conserve water. Some salts pass through the gut without being absorbed. Salts that are absorbed are excreted, mostly through the gills but also in the urine. (*b*) Freshwater fishes are in the reverse situation: The outside water has a very low salinity, so they tend to gain water by osmosis. To avoid swelling up, they refrain from drinking and produce large amounts of dilute urine. Salts are absorbed by the gills to replace those lost in the urine.

FIGURE 4.15 Sea turtles have glands near the eyes that excrete excess ions, producing salty "tears." This is a hawksbill turtle (*Eretmochelys imbricata*).

Marine birds and reptiles, and some marine plants, also have special cells or glands to rid themselves of excess salt (Fig. 4.15). Marine plants and most algae have the added advantage of a fairly rigid cell wall that helps them resist the swelling caused by osmotic water gain.

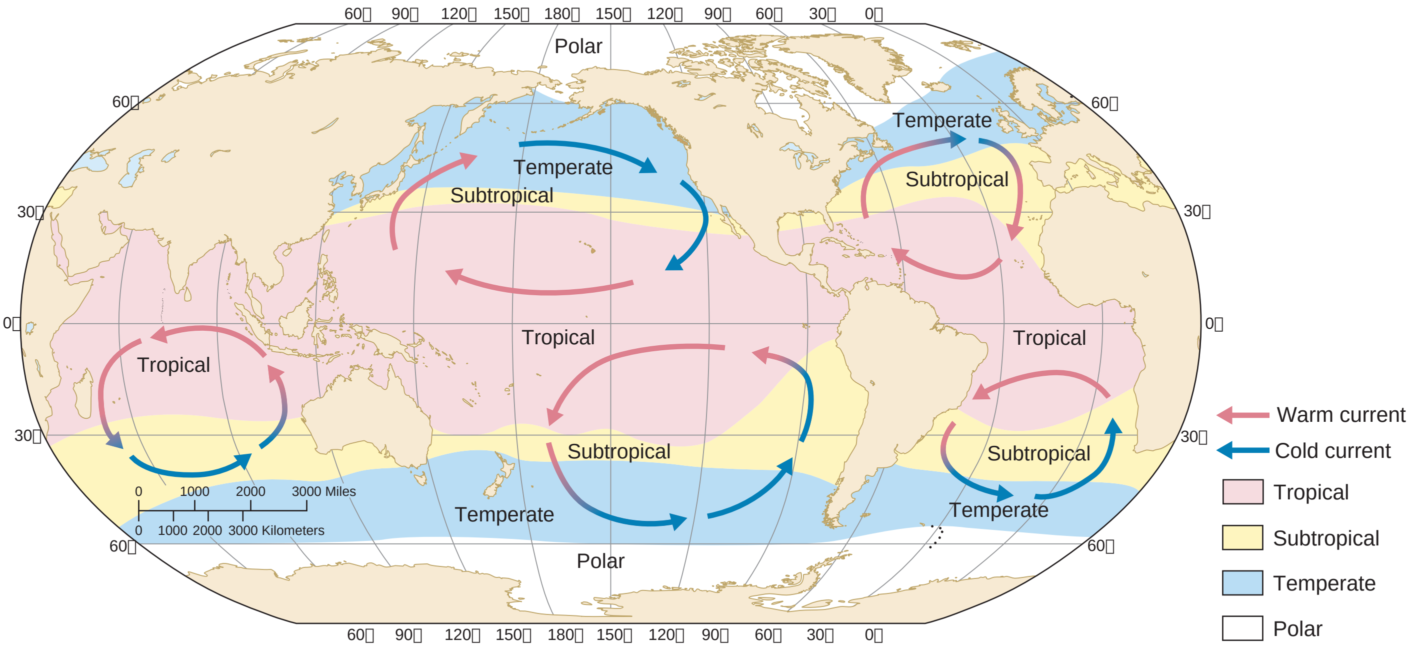
Temperature

Organisms are greatly affected by temperature. Metabolic reactions proceed faster at high temperatures and slow down dramatically as it gets colder. A general rule of thumb is that most reactions occur about twice as fast with a 10°C (18°F) rise in temperature. At extreme temperatures, however, most enzymes cease to function properly.

Most marine organisms are adapted to live in particular temperature ranges. Many polar species, for instance, have enzymes that work best at low temperatures, and they cannot tolerate warm water. The reverse is true of many tropical species. As a result, temperature plays a major role in determining where different organisms are found in the ocean (Fig. 4.16).

Organisms are often categorized according to how their metabolism affects their body temperature. All organisms generate metabolic heat, but in most organisms this heat is quickly lost to the environment and does not raise body temperature. These organisms are known as **ectotherms** and are commonly called "cold-blooded." In **endotherms,** on the other hand, metabolic heat is retained and raises the body temperature above that of the surroundings. Endotherms are often called "warm-blooded." Endotherms include mammals, birds, and some large fishes, including some tunas and sharks (see "Swimming: The Need for Speed," p. 341).

Another way to categorize organisms is by whether they can keep their body temperature more or less constant regardless of the temperature of the environment. The body temperature of **poikilotherms** changes along with the temperature of the surroundings. All ectotherms are also poikilotherms. As the temperature of the water rises and falls so does their body temperature, and consequently


60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
Polar
60°
60°
Temperate
Subtropical
Temperate
Subtropical
30°
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0°
Tropical
Tropical
Tropical
30°
30°
Subtropical
Subtropical
Temperate
Temperate
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
60°
60°
Polar
60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
Warm current
Cold current
Tropical
Subtropical
Temperate
Polar

FIGURE 4.16 Marine organisms are often restricted to specific regions that correspond to average water temperatures. The major divisions are the polar, temperate, subtropical (or warm temperate), and tropical regions. The boundaries of these regions are not absolute and change slightly with the seasons and shifts in current patterns. This map refers only to surface waters; deep water is uniformly cold.

Volume	Surface area	S/V ratio
1 cm^3	6 cm^2	6:1
8 cm^3	48 cm^2	6:1
8 cm^3	24 cm^2	3:1

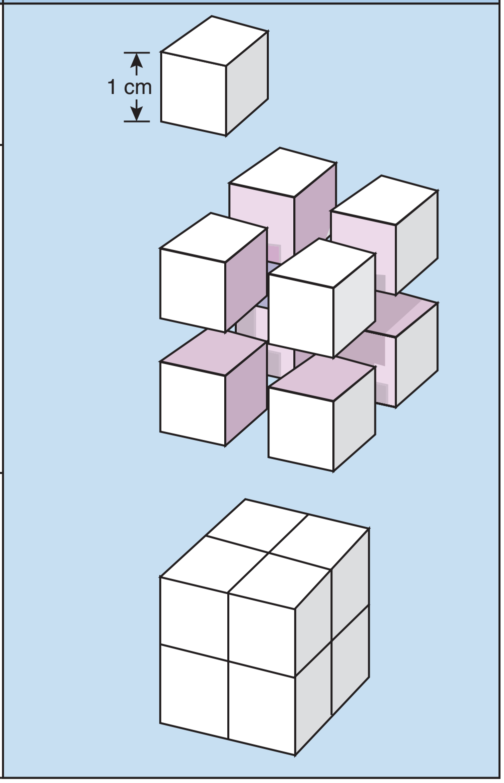


FIGURE 4.17 A cube that is 1 cm on a side (top) has a volume of 1 cm^3 and, because it has six sides , a surface area of 6 cm^2. Eight such cubes (middle) will, of course, have both eight times the volume and eight times the surface area, so the ratio of the surface area to the volume of the cubes, or surface-to-volume (S/V) ratio, will stay the same: 6:1. If the eight cubes are combined into a single large one (bottom), half the surfaces are hidden in the interior. The S/V ratio, like the surface area, is reduced by half, to 3:1. A large cube, therefore, has a lower S/V ratio than a small one.

their metabolic rate. This can make ectothermic animals sluggish if the water is colder than they are used to. Warm-blooded, or endothermic, tunas and sharks are also poikilotherms. Although they retain metabolic heat generated by their large muscles and are warmer than the surrounding water, their internal temperature still goes up and down as water temperature changes.

Mammals and, to a lesser extent, birds are able to regulate their internal temperature so that it stays much the same even when the external temperature varies. They are called **homeotherms.** Being endotherms, they retain heat, but they also control their metabolism, producing more heat as needed by burning up fats and other energy-rich molecules. This allows them to remain highly active regardless of water temperature, but it also requires a lot of energy, so homeotherms need to eat more often than poikilotherms. To reduce the "heat bill"—the energy cost of maintaining their body temperature—mammals and birds are insulated with feathers, hair, or blubber.

Surface-to-Volume Ratio

Adaptations to salinity and temperature are needed because salts and heat can flow in and out of organisms—if organisms were not affected by their environment, they would not have to adapt. Organisms also exchange nutrients, waste products, and gases with the environment. Such materials often move in and out across the surface of marine organisms, so the amount of surface area is very important. More precisely, it is the amount of surface area relative to the total volume of an organism—in other words, the **surface-to-volume ratio,** or **S/V ratio**—that determines how rapidly heat and materials flow in and out.

One thing that determines the S/V ratio is the size of the organism. As organisms grow larger, their volume increases faster than their surface area. Small organisms have a larger S/V ratio than big ones (Fig. 4.17). Small organisms, especially single-celled ones, can therefore rely on simple diffusion across their surfaces for the exchange of materials. Larger organisms must develop supplementary mechanisms, like respiratory and excretory systems.

PERPETUATING LIFE

One of the most basic characteristics of living things is the ability to reproduce—to generate offspring similar to themselves. Any life form that failed to replace itself with new individuals of its own kind would soon vanish from the planet. It is only by reproducing that a species ensures its own survival.

Organisms must do two things when they reproduce. First, they must produce new individuals to perpetuate the species. Second, they must pass on to this new generation the characteristics of the species in the form of genetic information. The transfer of genetic information from one generation to the next is called **heredity.**

Organisms achieve the first objective, the production of offspring, in many different ways. But there are relatively few ways through which they pass on genetic information. This similarity of hereditary mechanisms is evidence that all living things are fundamentally related.

Modes of Reproduction

The primary way that individual cells reproduce is by dividing to form new **daughter cells** (Fig. 4.18). In prokaryotes, where the DNA that carries the genetic information is not enclosed in a nucleus, the cell divides into two new ones by a simple process called **cell fission.** Before dividing, the cell copies, or **replicates,** its DNA. Each daughter cell gets one of the copies, as well as the rest of the cellular machinery it needs to survive.

In eukaryotes the DNA lies on several different chromosomes. Before a cell divides, each chromosome is replicated. The most common form of eukaryotic cell division, **mitosis,** is a

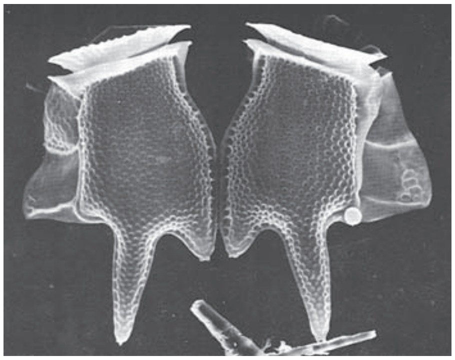


FIGURE 4.18 Two cells of a microscopic organism called a dinoflagellate *(Dinophysis tripos)*. These cells were formed by the division of a single cell. The two cells, joined here, will soon separate.

complex process that takes place in the nucleus. Mitosis ensures that each daughter cell gets a copy of every chromosome. As in bacterial cell division, the end result is two daughter cells that are exact duplicates of the original, with the same genetic information.

Asexual Reproduction Cell division is the primary way that single-celled organisms reproduce. Because a single individual can reproduce itself without the involvement of a partner, this form of reproduction is called **asexual reproduction.** All forms of asexual reproduction are similar in that the offspring inherit all the genetic characteristics of the parent. They are, in fact, exact copies, or **clones.**

Many multicellular organisms also reproduce asexually. Some sea anemones, for example, simply split in half to create two smaller anemones. This process is known as **fission.** Another common form of asexual reproduction is **budding.** Instead of dividing into two new individuals of equal size, the parent develops small growths, or **buds,** that eventually break away and become separate individuals (Fig. 4.19*a*). Many plants reproduce asexually by sending out various kinds of runners that take root and then sever their connection to the parent (Fig. 4.19*b*). Because it is so common in plants, asexual reproduction is sometimes called **vegetative reproduction,** even when it occurs in animals.

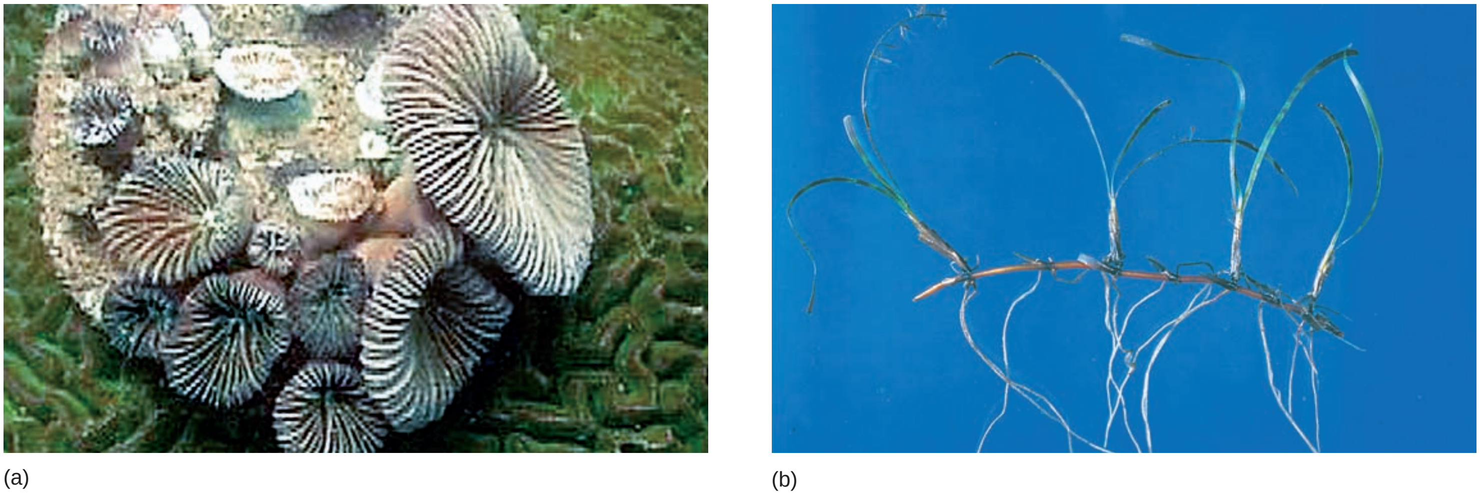
> Asexual, or vegetative, reproduction can be performed by single individuals and produces offspring that are genetically identical to the parent.

Sexual Reproduction Most multicellular and some unicellular organisms reproduce part or all of the time by **sexual reproduction,** in which new offspring arise from the union of two separate cells called **gametes.** Usually each of the gametes comes from a different parent.

Organisms that reproduce sexually have a special kind of tissue called **germ tissue.** Whereas all the other cells in the body divide only by mitosis, germ cells are capable of a second type of cell division, **meiosis.**

In most of the cells of eukaryotic organisms the chromosomes occur in pairs, with each chromosome of a pair storing similar genetic information. Such cells are said to be **diploid,** designated **2*n*.** Meiosis produces daughter cells that have copies of only half the parents' chromosomes—one of each pair. Cells with half the normal number of chromosomes are called **haploid,** designated ***n*** or **1*n*.** The haploid daughter cells produced in meiosis are the gametes. In some seaweeds and microscopic organisms, all the gametes are the same. Most organisms, however, have two types of gametes: female gametes called **eggs** and male gametes called **sperm** (Fig. 4.20). In animals the germ tissue is usually contained in **gonads,** the organs that produce the gametes. **Ovaries** are the female gonads, which produce eggs. In animals the male gonads, or **testes,** produce sperm. Seaweeds also have gonads that produce sperm, while in flowering plants sperm develop within pollen, which is produced by organs in the flower called anthers.

Eggs are large cells, usually an organism's largest. They contain all the cellular machinery—organelles and cytoplasm—characteristic of regular cells. The eggs of many species also contain large amounts of energy-rich yolk. Sperm, by contrast, are usually an organism's smallest cells, with almost no cytoplasm and few of the typical organelles. Sperm are little more than tiny



(a) (b)

FIGURE 4.19 (*a*) Budding is a common form of reproduction in marine animals, including this mushroom coral (*Fungia fungites*). The parent coral is nearly dead, but the many buds on its surface will soon break off and become free-living adults (see Fig. 14.3*a*). (*b*) This seagrass (*Halodule pinifolia*) reproduces asexually by sending out rhizomes, or "runners" that take root and form new plants.

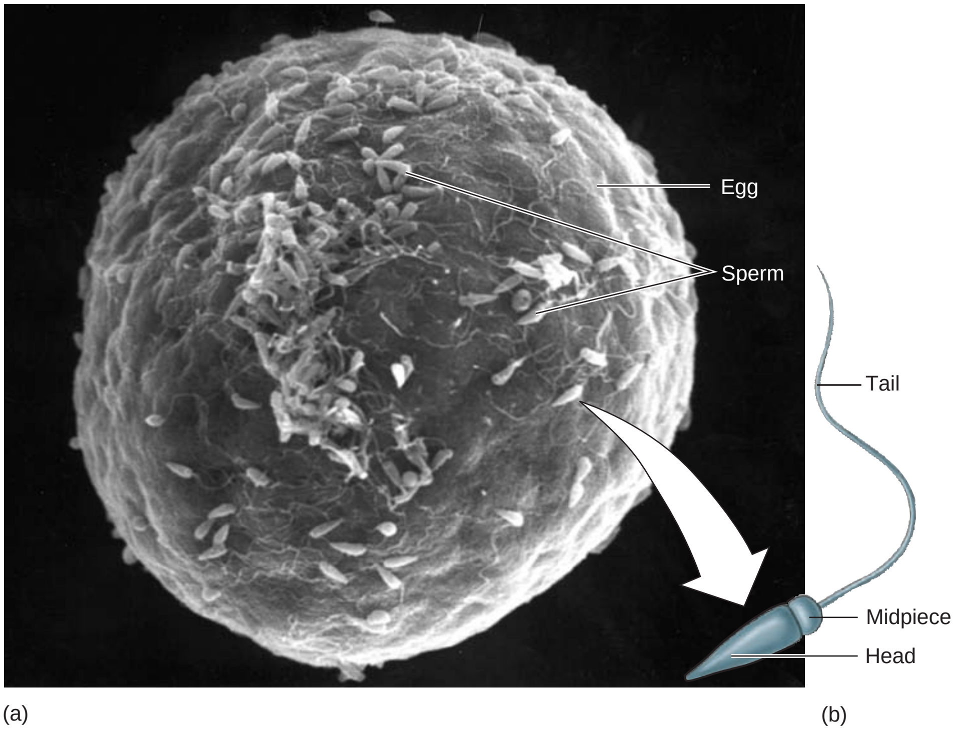


FIGURE 4.20 (*a*) The egg of the variegated sea urchin *(Lytechinus variegatus)* is many times larger than sperm from the same species. Though many sperm surround the egg, only one will fertilize it. The egg contains a large amount of cytoplasm and the organelles characteristic of other cells. It also contains yolk to nourish the developing embryo. (*b*) The head of a sperm cell is made up almost entirely of the cell nucleus and contains the genetic material. The midpiece contains mitochondria that power the tail, or flagellum, with which the sperm swims.

packages of chromosomes equipped with mitochondria-powered flagella that enable the sperm to swim.

> Mitosis, the most common form of cell division, produces two daughter cells that are identical to the original cell. Meiosis, on the other hand, produces daughter cells that have half the normal number of chromosomes—that is, they are haploid. These daughter cells are called gametes. Eggs and sperm are the female and male gametes, respectively.

Sperm are attracted to eggs from the same species. When egg and sperm come into contact, they fuse; in other words, **fertilization** occurs. The genetic material contained in the two gametes combines. Since both haploid gametes had $1n$ chromosomes—or half the normal number—the fertilized egg, called a **zygote,** is back to the normal diploid, or $2n$, number of chromosomes. It has DNA from *both* parents, however, and is therefore different from either. This **recombination** of genetic information to produce offspring that differ slightly from their parents is the most important feature of sexual reproduction.

> In sexual reproduction two gametes, usually eggs and sperm, fuse to create a genetically distinct individual.

The fertilized egg begins to divide by ordinary mitosis. Now called an **embryo,** it is nourished by the yolk. Through an extraordinarily complex process called embryological development, the embryo eventually becomes a new adult of the species. Along the way, most marine organisms pass through immature, or **larval,** stages that often look completely different from the adults (see Figs. 7.39 and 15.11).

Reproductive Strategies

The goal of reproduction for any organism is to pass its hereditary characteristics on to a new generation. There is a nearly endless variety of ways to achieve this (Fig. 4.21). Some species release millions of eggs and sperm into the water, where fertilization occurs, and have no further interaction with their offspring. This is called **broadcast spawning.** Others issue only a few offspring and invest a lot of time and energy in caring for them. Some species have many different larval stages, whereas others develop directly from egg to adult. Some reproduce asexually, some reproduce sexually, and some do both. In sexually reproducing species, males and females may always be separate individuals, or there may be **hermaphrodites,** individuals that have both male and female reproductive organs either at the same time or at different times of life.

The particular combination of methods used by a given species is called its **reproductive strategy.** The strategy used by a species depends on its size, on where and how it lives, on what kind of organism it is—in fact, on just about everything about it and its environment.

THE DIVERSITY OF LIFE IN THE SEA

There are so many different living things in the sea that it almost boggles the mind. From microscopic bacteria to gigantic whales, marine organisms come in all shapes, sizes, and colors. The ways in which they live are just as varied. Making sense of all this **diversity** might seem a hopeless task. Fortunately, there is a unifying concept that helps make the bewildering diversity of life comprehensible. This concept is the **theory of evolution.** Remember that scientists do not use the term "theory" lightly. Evolution, the gradual alteration of a species' genetic makeup, is supported by a vast body of evidence. The *ways* in which evolution occurs, on the other hand, never cease to fascinate biologists.

Natural Selection and Adaptation

Evolution occurs because individual organisms have genetic differences in their ability to find food and avoid being eaten, in their success at producing offspring, in their metabolism, and in countless other attributes. The best-adapted individuals, those most successful at meeting the challenges of the environment,

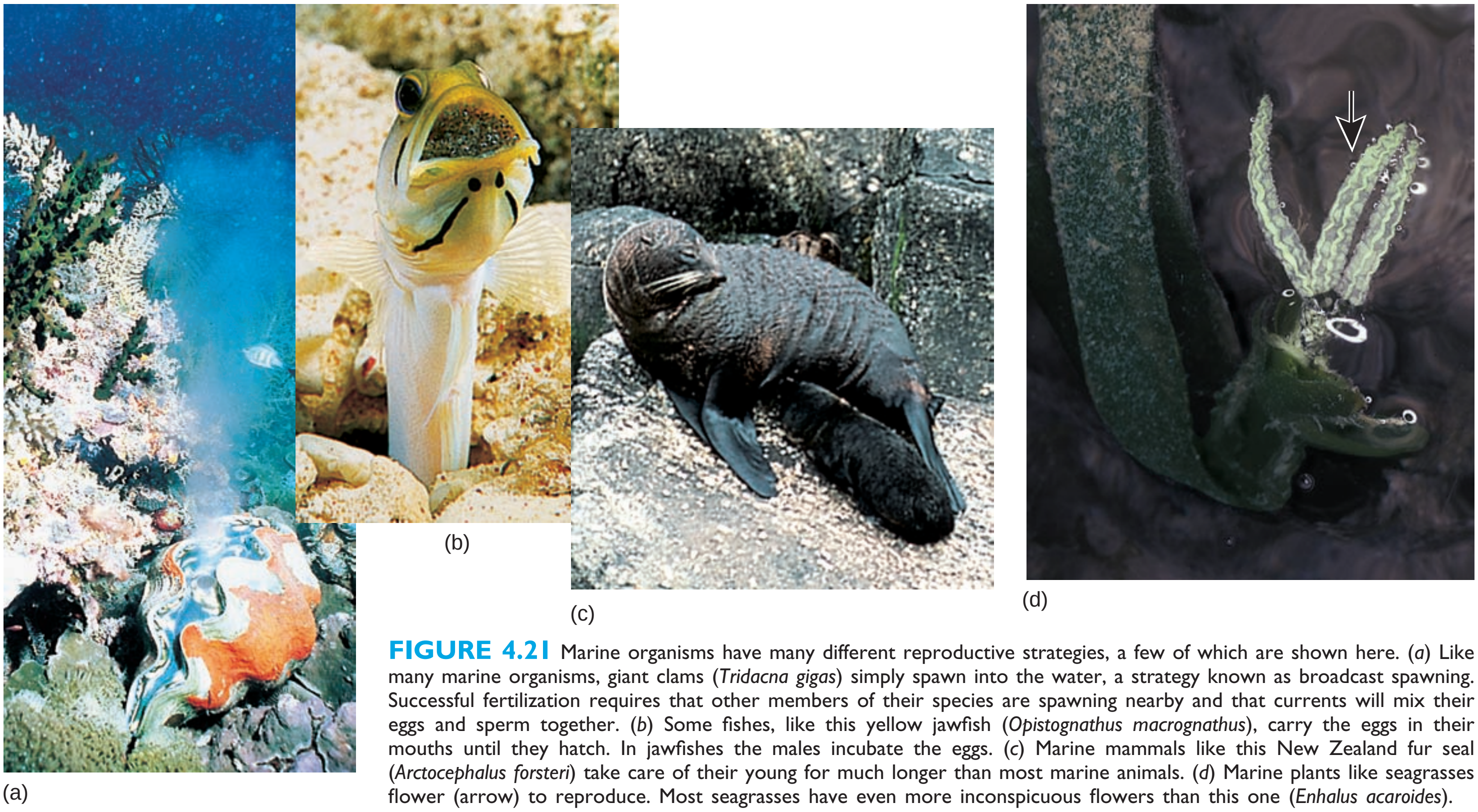


FIGURE 4.21 Marine organisms have many different reproductive strategies, a few of which are shown here. (*a*) Like many marine organisms, giant clams (*Tridacna gigas*) simply spawn into the water, a strategy known as broadcast spawning. Successful fertilization requires that other members of their species are spawning nearby and that currents will mix their eggs and sperm together. (*b*) Some fishes, like this yellow jawfish (*Opistognathus macrognathus*), carry the eggs in their mouths until they hatch. In jawfishes the males incubate the eggs. (*c*) Marine mammals like this New Zealand fur seal (*Arctocephalus forsteri*) take care of their young for much longer than most marine animals. (*d*) Marine plants like seagrasses flower (arrow) to reproduce. Most seagrasses have even more inconspicuous flowers than this one (*Enhalus acaroides*).

produce more offspring on average than those that are not so well adapted. This process was called **natural selection** by Charles Darwin, the nineteenth-century English naturalist who along with another Englishman, Alfred Wallace, first proposed the modern theory of evolution.

The best-adapted individuals not only produce more offspring, they also pass their favorable characteristics on to those offspring. The favorable traits therefore become more common, and over generations the population as a whole gradually becomes more similar to the best-adapted individuals. Thus, the result of natural selection is that the population continually adapts to its environment—that is, it evolves.

> Natural selection occurs when some members of a population survive and reproduce more successfully than others. Evolution is the genetic change in the population that results because these more successful individuals pass their favorable characteristics on to their young.

Every population is constantly adapting to its environment. The world is an ever-changing place, however, and organisms are always being faced with new challenges. Populations either adapt to the changes in the environment or become extinct, making way for others. As a result, evolution is an endless process.

Classifying Living Things

The adaptation of various populations to different environments has produced a fantastic variety of life forms. It is difficult to study and discuss the millions of life forms on earth unless we first classify them, or sort them into groups. One of the goals of biological classification is to give a universally accepted name to different types of organisms so that scientists from all over the world can call a species by the same name.

The Biological Species Concept We have loosely defined a species as a "type" of organism, but what exactly does that mean? After all, fishes are all the same general type of animal, but a sailfish is obviously not the same species as a tuna (see Figs. 1.16 and 1.18). No definition is perfect, but here we will define species as populations of organisms that have common characteristics and can successfully breed with each other. This definition is often referred to as the **biological species concept.**

Successful breeding means that the offspring produced are fertile and can themselves propagate the species. Dogs, to use a familiar example, are all the same species because all breeds of dog—no matter how different they may look—can interbreed to produce fertile offspring. Organisms that cannot breed with each other are not members of the same species no matter how similar they look. When two populations are unable to interbreed successfully, they are said to be **reproductively isolated.**

> A species is a population of organisms that share common characteristics, can breed with each other, and are reproductively isolated from other populations.

Biological Nomenclature Organisms are identified biologically by two names, the name of their **genus** and a species name

EYE ON SCIENCE

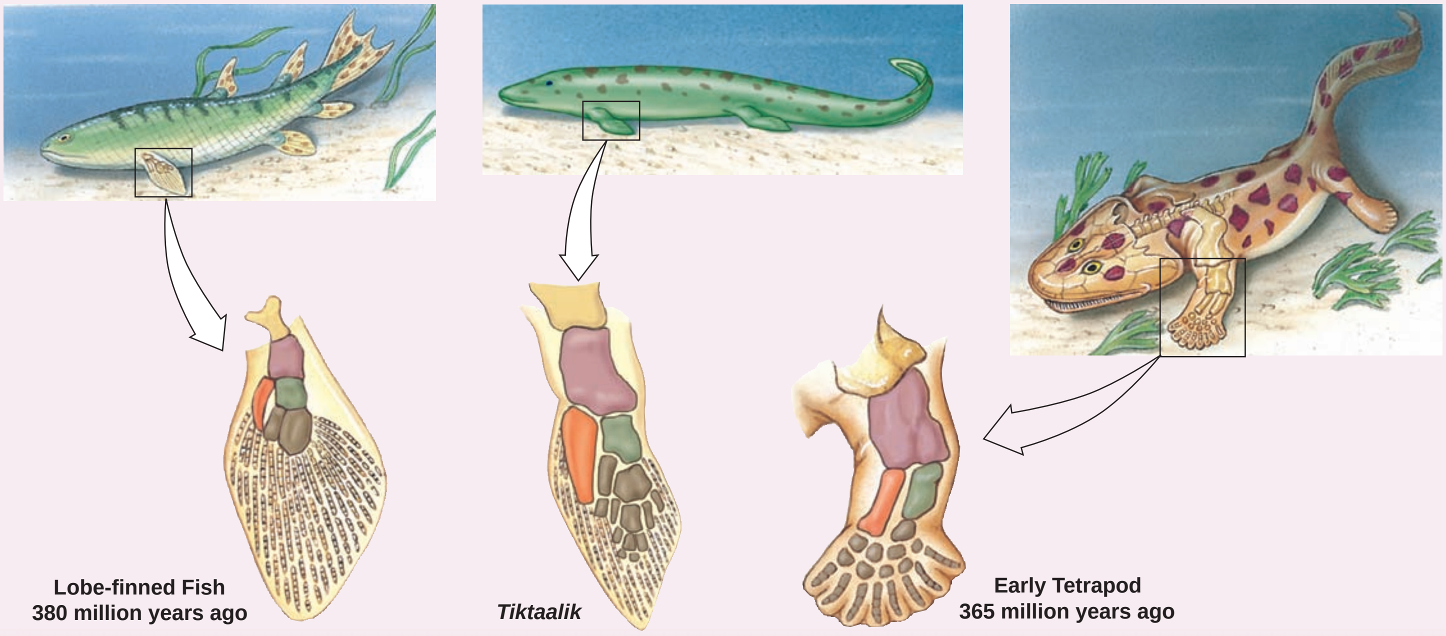
When Fishes Stepped on Land

Organisms evolve in tiny steps, with each change only incrementally different from before, so a key challenge in evolutionary biology is to understand how complex and radically different new structures could have evolved. Fins are great for swimming, and legs are great for walking, but how did animals get from one to the other while still being able to catch food, avoid predators, and find mates every step of the way? Recent breakthroughs have helped us understand how fishes moved onto land to become tetrapods (animals with two pairs of limbs).

Paleontologists recently discovered fossils of a fish *(Tiktaalik roseae)* that appears very close to the so-called missing link between fishes and the first land vertebrates. *Tiktaalik* lived about 375 million years ago, 10–15 million years before the earliest known fossil tetrapods. The arrangement of bones in *Tiktaalik's* fins is almost perfectly intermediate between the limbs of early tetrapods and the fins of lobe-finned fishes, the ancestors of tetrapods. In particular, *Tiktaalik's* fin bones foreshadow the elbow, wrist, and fingers of tetrapods. *Tiktaalik* was probably unable to walk, but it could at least use its fins to do push-ups. *Tiktaalik*, whose discoverers affectionately refer to as a "fishopod," had other features that would be refined in tetrapods, such as the beginnings of the first neck. Scientists doubt that *Tiktaalik* is the direct ancestor of tetrapods, but it is probably a very close cousin. Every summer *Tiktaalik's* discoverers return to the Canadian Arctic where they found its fossils in hope of new discoveries about the emergence of tetrapods, which 300 million years later would return to the sea as whales (see "The Whales That Walked to Sea," p. 192).

Meanwhile, biologists are learning the genetic basis for these changes. The key is that evolution does not have to completely reinvent the wheel—or the limb. The genome is flexible enough that the same basic system, with only minor tweaks, can control the development of a range of different structures. The earliest fishes did not have paired fins on the side, only median fins, single fins along the midline like the dorsal fin of sharks (see "Cartilaginous Fishes," p. 153). In today's sharks the dorsal fin and paired fins develop from different cells in different parts of the embryo, but biologists recently showed that the same genetic programs control the embryonic development of both. These genes are also involved in the development of median fins in lampreys, primitive fishes that branched off before paired fins emerged (see "Jawless Fishes," p. 153), and the development of wings in chick embryos. Thus, the same genetic mechanism controls the development of median fins, paired fins, limbs, and wings. Paired fins and limbs did not evolve from scratch, but emerged through the application of the molecular system that was already producing median fins. The researchers are testing this hypothesis by studying lancelets, the nearest invertebrate relatives of vertebrates (see "Chordates Without a Backbone," p. 145).

For more information, explore the links provided on the Marine Biology *Online Learning Center.*



or, more correctly, **species epithet.** A genus is a group of very similar species. Dogs, for example, have the scientific name *Canis familiaris*. They are closely related to other species in the genus *Canis,* like wolves, *Canis lupus,* and coyotes, *Canis latrans*. Similarly, the genus *Balaenoptera* contains several related species of whales, including the blue whale, *Balaenoptera musculus;* the fin whale, *Balaenoptera physalus;* and the minke whale, *Balaenoptera acutorostrata.* This two-name system is called **binomial nomenclature.** It was first introduced in the eighteenth century by the Swedish biologist Carolus Linnaeus. At that time Latin was the language of scholars, and Latin is still used for scientific names, along with Greek. By convention, binomial names are always underlined or italicized. The first letter of the generic name, but not the species epithet, is capitalized. When the name of the genus has been previously mentioned it may be abbreviated. Thus, the blue whale could be identified as *B. musculus*. The species epithet is never used by itself, but only in conjunction with the genus name or initial.

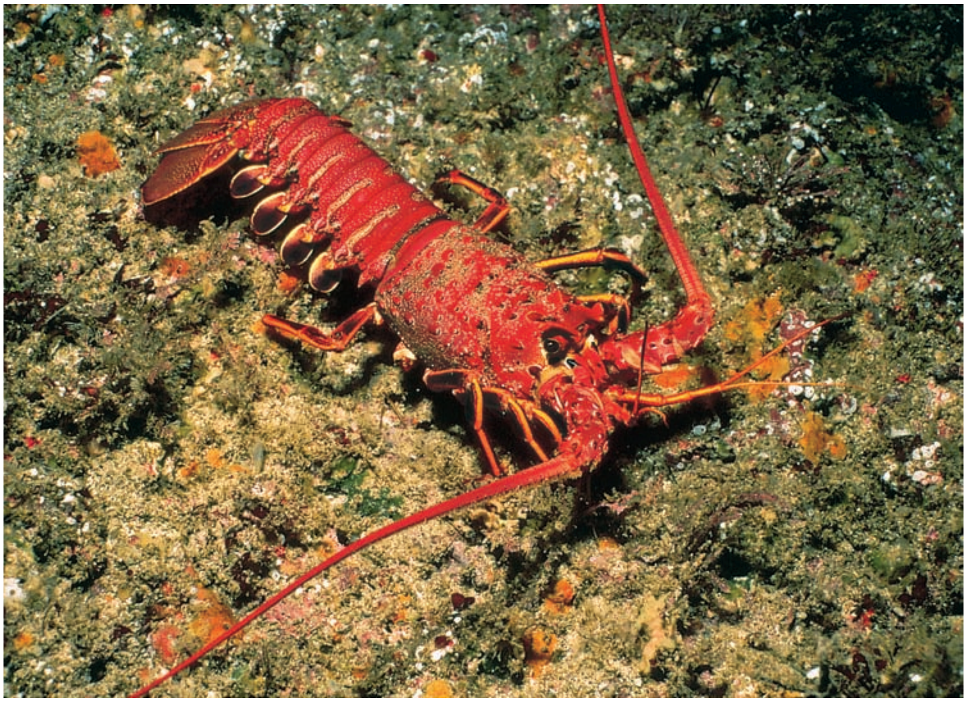


FIGURE 4.22 *Panulirus interruptus,* the Pacific spiny lobster, is sometimes called a rock lobster or a crayfish.

Students often ask why biologists have to use complicated, hard-to-pronounce Latin or Greek names rather than ordinary common names. The trouble with common names is that they are not very precise. The same common name may be applied to different species, and the same species may have different common names. The name "spiny lobster" (Fig. 4.22), for example, is applied to many different species that are not even all in the same genus. Australians call spiny lobsters "crayfish." Americans reserve the name "crayfish" for freshwater relatives of lobsters. Things get even more confusing when people speak different languages. In Spanish, spiny lobsters are called *langostas,* which can also refer to grasshoppers. Another example is the name "dolphin," which is applied not only to the lovable relatives of whales but also to a delicious game fish. Dolphin fish are called *dorado* in Latin America and *mahimahi* in Hawai'i. At the local seafood grotto this confusion is only a minor annoyance. To biologists, however, it is essential to precisely identify whatever species they are discussing. The use of scientific names that are accepted worldwide avoids confusion.

Confusion over common names can have practical implications as well. After a dive on a coral reef near Australia, one of the authors mentioned to his dive buddy that he had seen a gray reef shark. Gray reef sharks, although not so dangerous as to force you out of the water, can be aggressive and merit some attention and respect. The diving partner, who was familiar with the area, replied that the shark was not a gray reef, but a "graceful whaler." "Looks just like a gray reef shark to me," said the author but, reassured, he continued diving, blissfully ignoring the "graceful whalers" that swam by. Only later did he discover that "graceful whaler" was just a local name for the gray reef shark, *Carcharhinus amblyrhynchos* (see Fig. 8.5*a*)!

Phylogenetics: Reconstructing Evolution The goals of biological classification include not only assigning agreed-upon names to organisms but also grouping them according to their relatedness. Most people instinctively understand that a seal is related to a sea lion, for example, or that oysters and clams are related. They might be hard-pressed, though, to explain exactly what they mean by "related." To a biologist, saying that two groups of organisms are "related" means that they share a common evolutionary history, or **phylogeny.** In particular, it means that both groups evolved from a common ancestral species. Closely related groups evolved from common ancestors relatively recently, while the common ancestors of distantly related groups occurred further in the past. The study of such evolutionary relationships is called **phylogenetics.**

It is almost always difficult to determine the phylogenetic relationships among organisms. Very few groups have a good record of fossils that trace their evolutionary history. Usually the fossil record is incomplete or nonexistent. Biologists have to try to piece together an organism's evolutionary history from other evidence. Body structure, reproduction, embryological and larval development, and behavior all provide clues. Biologists rely increasingly on molecular studies and, in particular, on DNA and RNA sequences. Because evolution is genetic change by definition, the study of the nucleic acids that store organisms' genetic information reveals a great deal about evolution. Unfortunately, different methods of studying phylogeny frequently yield different results, and experts in a particular group often disagree about its phylogeny (Fig. 4.23). Classification schemes change and new arguments arise as fresh information becomes available.

As noted previously, biological classification seeks to group organisms according to their relatedness. Species that are very

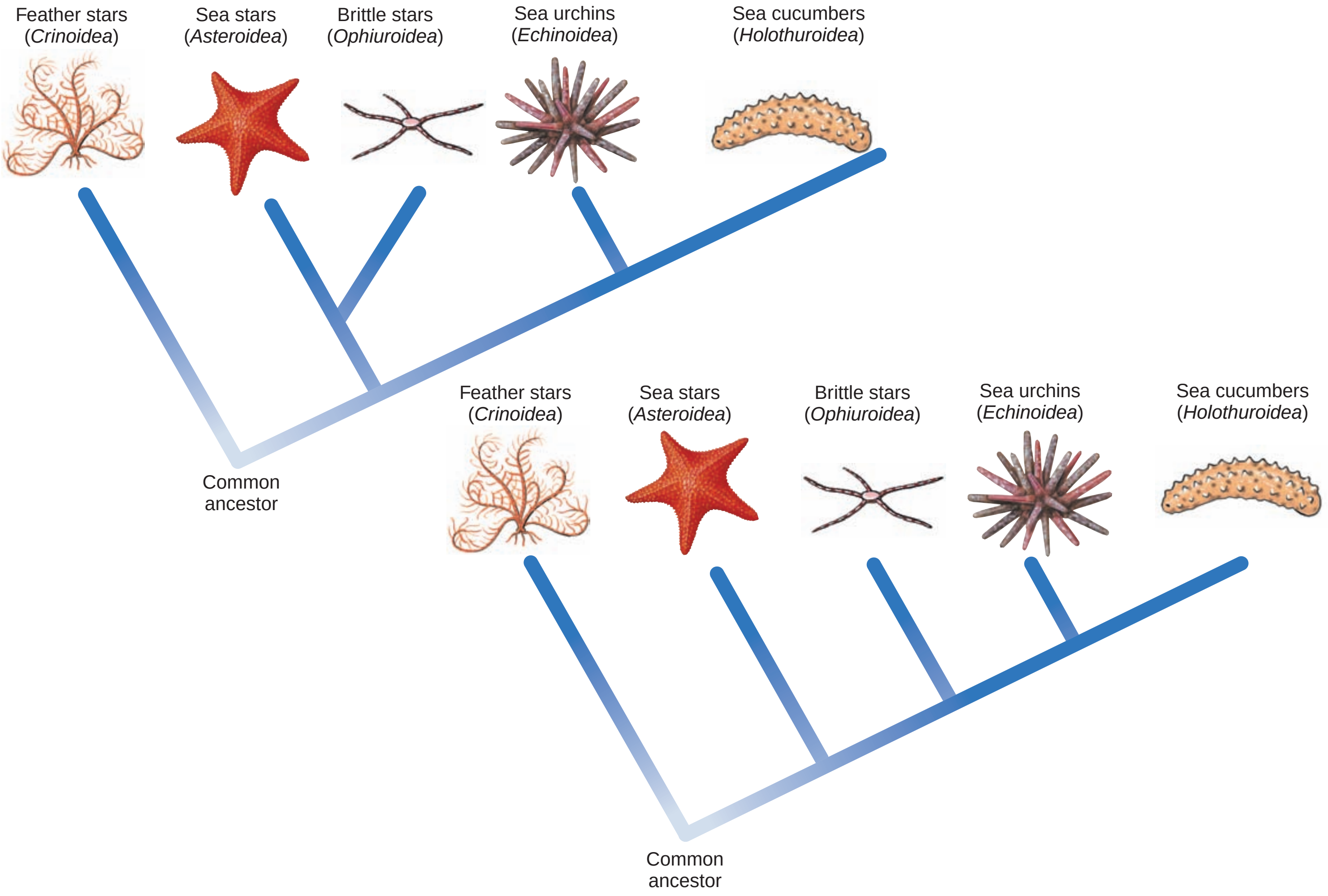

Feather stars (Crinoidea)
Sea stars (Asteroidea)
Brittle stars (Ophiuroidea)
Sea urchins (Echinoidea)
Sea cucumbers (Holothuroidea)
Common ancestor
Feather stars (Crinoidea)
Sea stars (Asteroidea)
Brittle stars (Ophiuroidea)
Sea urchins (Echinoidea)
Sea cucumbers (Holothuroidea)
Common ancestor

FIGURE 4.23 Alternative proposals for the phylogeny of the major groups of echinoderms. Both schemes accept that feather stars diverged early from the common ancestor of all echinoderms and that urchins and sea cucumbers are more closely related to each other than to other echinoderms. The proposals differ, however, with regard to the phylogeny of sea stars and brittle stars. Conflicting hypotheses like these are common in phylogenetics.

closely related, for example, are grouped into the same genus. Genera with similar phylogenies can be grouped together into a larger group, called a family. This process can be continued to sort organisms into progressively larger groups. All the members of a group, or **taxon** (plural, **taxa**), have certain common characteristics and are thought to share a common ancestry. Taxa are systematically arranged in a hierarchy that extends from the most general classification, the domain, down to the species (Table 4.2).

The Tree of Life In centuries past, all known organisms were classified as either plants (kingdom **Plantae**) or animals (kingdom **Animalia**). As biologists learned more about the living world, however, they discovered many organisms that didn't fit, and the classification scheme was changed to recognize additional kingdoms. A system of five kingdoms became widely accepted. In addition to the Animalia and Plantae, this traditional system included fungi (kingdom **Fungi**), bacteria (kingdom **Monera**), and protists (kingdom **Protista**). Fungi are multicellular, heterotrophic organisms that are neither plants nor animals. Protists are an extremely varied group of organisms, some plant-like and some animal-like, that includes both unicellular eukaryotes and multicellular seaweeds. Biologists now recognize that protists are a collection of taxa with different evolutionary histories rather than a true kingdom, although for convenience they are still often grouped together under the name "protists."

In recent years, studies of the RNA and cellular chemistry of prokaryotes have led biologists to conclude that there are two main groups of prokaryotes that are as different from each other as they are from all eukaryotic organisms (see "Prokaryotes," p. 87). To recognize this, some classification systems place these two groups of prokaryotes into two new kingdoms, the **Bacteria** and the **Archaea.** Other systems recognize a new taxon, the domain, that is even more general than the kingdom; in this system the Bacteria and Archaea are separate domains and each includes a number of different kingdoms. In this text we use the three-domain system of classification (Fig. 4.24), but not all biologists agree with this system.

Viruses are not included in this system because biologists are not sure whether they are alive (see "Viruses," p. 86). Viruses consist

Table 4.2 Biological Classification of Humans *(Homo sapiens)* and the Bottlenose Dolphin *(Tursiops truncatus)*

	Taxonomic Level	Example
Human		
	Domain	Eukarya
	Kingdom	Animalia
	Phylum	Chordata
	Class	Mammalia
	Order	Primates
	Family	Hominidae
	Genus	*Homo*
	Species	*Homo sapiens*
Dolphin		
	Domain	Eukarya
	Kingdom	Animalia
	Phylum	Chordata
	Class	Mammalia
	Order	Cetacea
	Family	Delphinidae
	Genus	*Tursiops*
	Species	*Tursiops truncatus*

Tursiops truncatus, the bottlenose dolphin.

Note: The term "division" is used in place of "phylum" in the classification of plants.

of little more than a handful of genes, encoded in either RNA or DNA, enclosed in a capsule of protein. Viruses are best known for causing disease, not only in humans but also in other organisms including marine ones. They also have a critical role in marine food chains (see "Trophic Levels and Energy Flow," p. 343).

Scientific Theory A *hypothesis* that is accepted as "true" for the time being because it has passed test after test and is supported by a large body of evidence.

- Chapter 1, p. 16

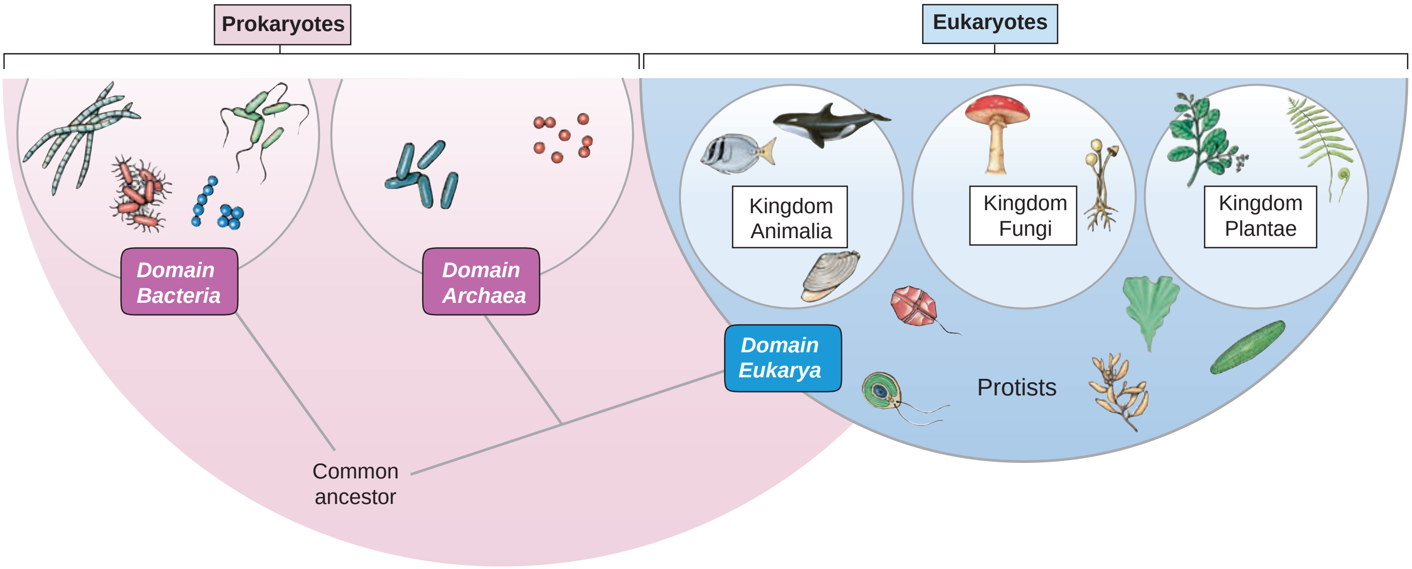

Prokaryotes
Eukaryotes
Domain Bacteria
Domain Archaea
Kingdom Animalia
Kingdom Fungi
Kingdom Plantae
Domain Eukarya
Protists
Common ancestor

FIGURE 4.24 The major groups of living things.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. During the day, algae carry out both photosynthesis and respiration, but at night, when there is no light, they can only perform respiration. Small, isolated tide pools on rocky shores are often inhabited by thick growths of seaweeds, which are algae. Would you expect the amount of oxygen in the water to differ between night and day? How?
2. The cells of some marine organisms are known to have high concentrations of ions found in minute amounts in seawater. Could these organisms accumulate the ions by diffusion? Formulate a hypothesis to explain how this accumulation is accomplished. How might this hypothesis be tested?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Allen, W., 2005. Challenging Darwin. *Bioscience,* vol. 55, no. 2, February, pp. 101–105. A dissident biologist offers controversial views of Darwin's theory of sexual selection.

Cohen, P., 2003. Renegade code. *New Scientist,* vol. 179, no. 2410, 30 August, pp. 34–37. Dogma has it that the genetic code has been handed down virtually unchanged to all living organisms, but this genetic operating system may have had some upgrades along the way.

Conniff, R. 2006/2007. Happy birthday, Linnaeus. *Natural History*, vol. 115, no. 15, December, pp. 42–47. Biologists around the world recently celebrated the 300th birthday of the founder of biological classification and nomenclature.

Darwin and evolution. *Natural History,* 2005, vol. 114, no. 9, November. Special issue with eight articles on Darwin and evolution.

Foer, J., 2005. Pushing Phylocode. *Discover,* vol. 26, no. 4, April, pp. 46–51. A controversial group of biologists wants to overturn the system of biological nomenclature that has lasted for centuries.

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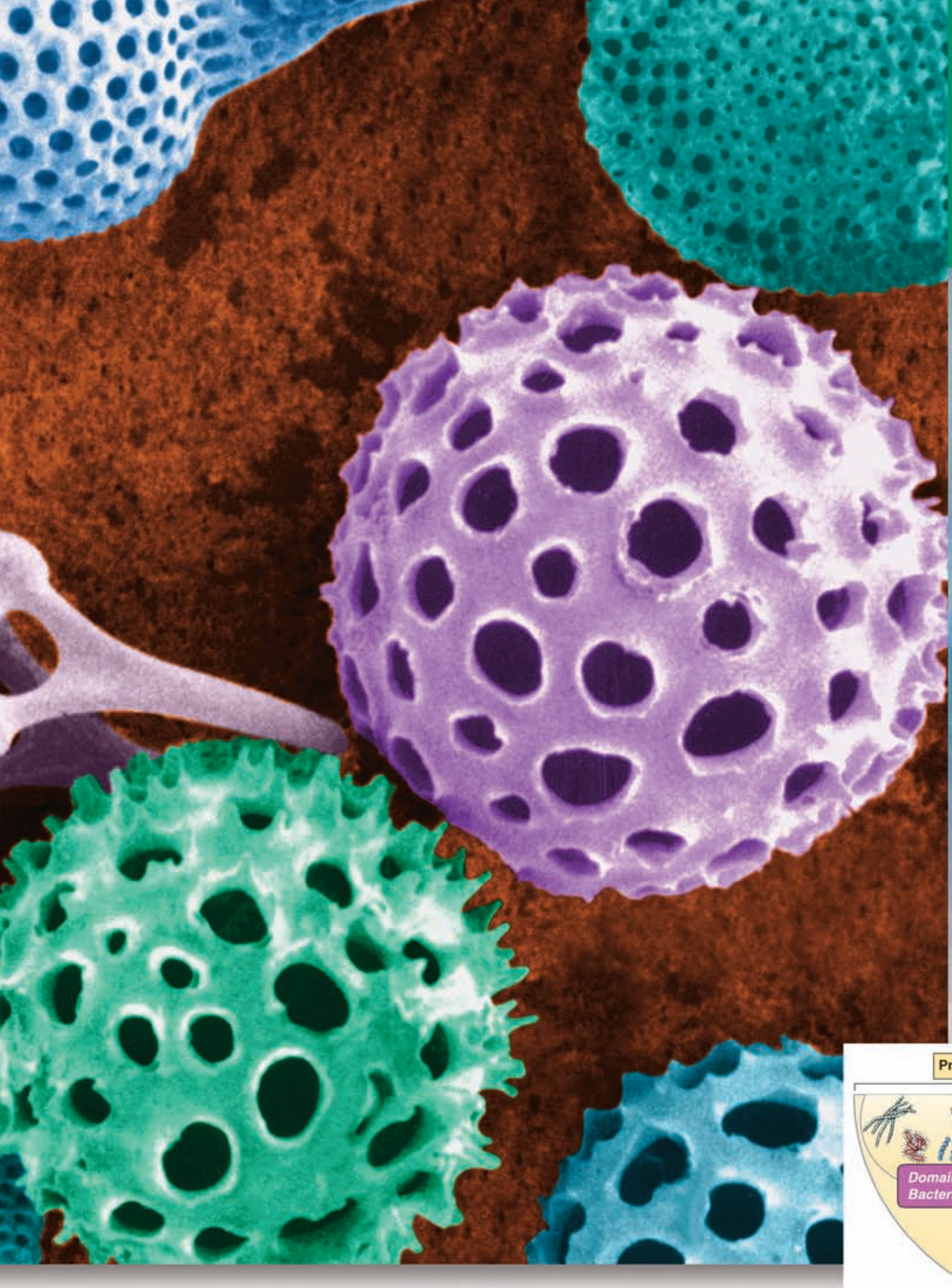
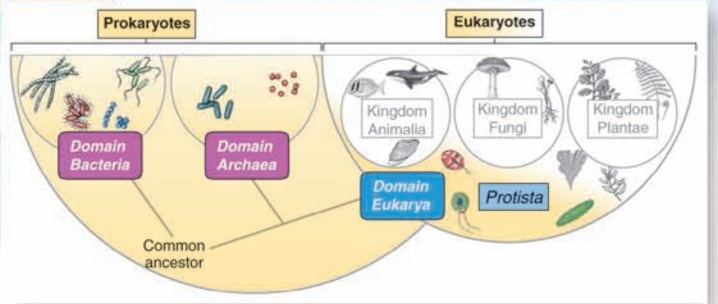
Part Two
The Organisms of the Sea

5
CHAPTER

The Microbial World



Radiolarian shells.



This chapter, the first in our survey of life in the ocean, is devoted to marine microorganisms, which are easily the most abundant forms of marine life. Microorganisms live everywhere in the ocean, from the deepest trenches to the highest tide pools. The microbial world includes an incredibly diverse assortment of organisms, and new microorganisms are discovered all the time. Except for being small, the various groups of microorganisms discussed in this chapter have little in common. All three biological domains, the most basic divisions of life (see "The Tree of Life," p. 82), include microorganisms. The diversity of the microbial world can be bewildering even to biologists. Indeed, much of the scientific debate about how to group organisms into kingdoms within domains centers on microorganisms.

Though marine microorganisms include some of the smallest and structurally simplest organisms, they have played critical roles in the evolution of life on our planet. Indeed, without microorganisms there would be no life on earth. Not only did life as we know it today evolve from microorganisms, but without them the planet could not support other forms of life.

Microorganisms are the most important **primary producers** in many marine environments, and directly or indirectly they feed most marine animals. Some microorganisms make essential nutrients available to primary producers, either for the first time or by recycling them. Others swim about in the water

Primary Producers Organisms that manufacture organic matter from CO_2, usually by photosynthesis.
- Chapter 4, p. 68

to ingest food very much as animals do and play critical roles in marine food webs.

VIRUSES

Viruses, remarkably, span the non-living and the living. Unlike living organisms, a virus is a particle not made up of a cell. Viruses consist of only a short chain of genetic material **(nucleic acid)** containing relatively few **genes** and protected by an outer protein coat, or **capsid.** They are parasites that reproduce and develop only when infecting a living cell. Viruses are minute, roughly between 20 and 200 nanometers (nm), 1 nm being equal to one-billionth of a meter, or 1,000 μm (see Appendix A for relative size). They can be seen only with the most powerful microscopes (Fig. 5.1).

Several types of viruses have been described. **Retroviruses** store their genetic information in the form of single-stranded **RNA,** in contrast to the double-stranded **DNA** of most viruses and all forms of life. Retroviruses are responsible for deadly human diseases, such as AIDS and some types of leukemia. Some viruses reproduce by attaching into a living cell and injecting their nucleic acid into the cell. The viral nucleic acid then commands the cell to produce, or replicate, copies of the virus, which are ultimately released as the infected cell bursts. The new generation of viruses then infects other cells or is released from the organism to infect new hosts. Another type, the **lysogenic** viruses, reproduce by inducing their nucleic acid to become part of the **genome** of the host cell, which then, sometimes long afterwards, directs the production not of host proteins but of new viruses. Many more viruses are then released as the infected cell is destroyed. Of particular importance in the ocean are **bacteriophages** (Fig. 5.1), viruses that specifically target—and destroy—bacteria.

Until recently, marine viruses have been practically ignored by marine scientists. They are nearly invisible, so it was not until the development of new techniques (see "Tiny Cells, Big Surprises," p. 92) that viruses were shown to be extremely common in marine environments and to play an important role in the complex cycles of life in the ocean. Though viruses are not referred to as living "organisms" in the strict sense of the word, viruses constitute the most abundant life-like particles in the ocean. Virus numbers in water samples can be determined by staining them with chemicals and observing them under a microscope, something that can be done on a research vessel. Their numbers in seawater samples can be staggering.

The abundance of viruses in the water is directly related to the abundance of microbial life, particularly bacteria, which they infect and destroy to reproduce. Viruses also infect other marine microbes that form part of the **phytoplankton,** very important primary producers in the ocean (see "Unicellular Algae," p. 93). The bursting of the cells of bacteria and phytoplankton as the result of viral infections also releases into the water large amounts of organic molecules and cell debris, which make up **dissolved organic matter (DOM).** DOM cannot be utilized as such by most organisms. It is, however, readily taken in by bacteria and other microbes. These microbes are eaten by small **zooplankton,** which are then eaten by larger zooplankton, so that the energy contained in DOM, a significant part of primary production by the phytoplankton, is not lost but ultimately is available to all kinds of animals, from small fishes to whales (see "The Microbial Loop," p. 344). The bursting of cells as a result of viral infections also releases some essential nutrients, which can then be made available to primary producers.

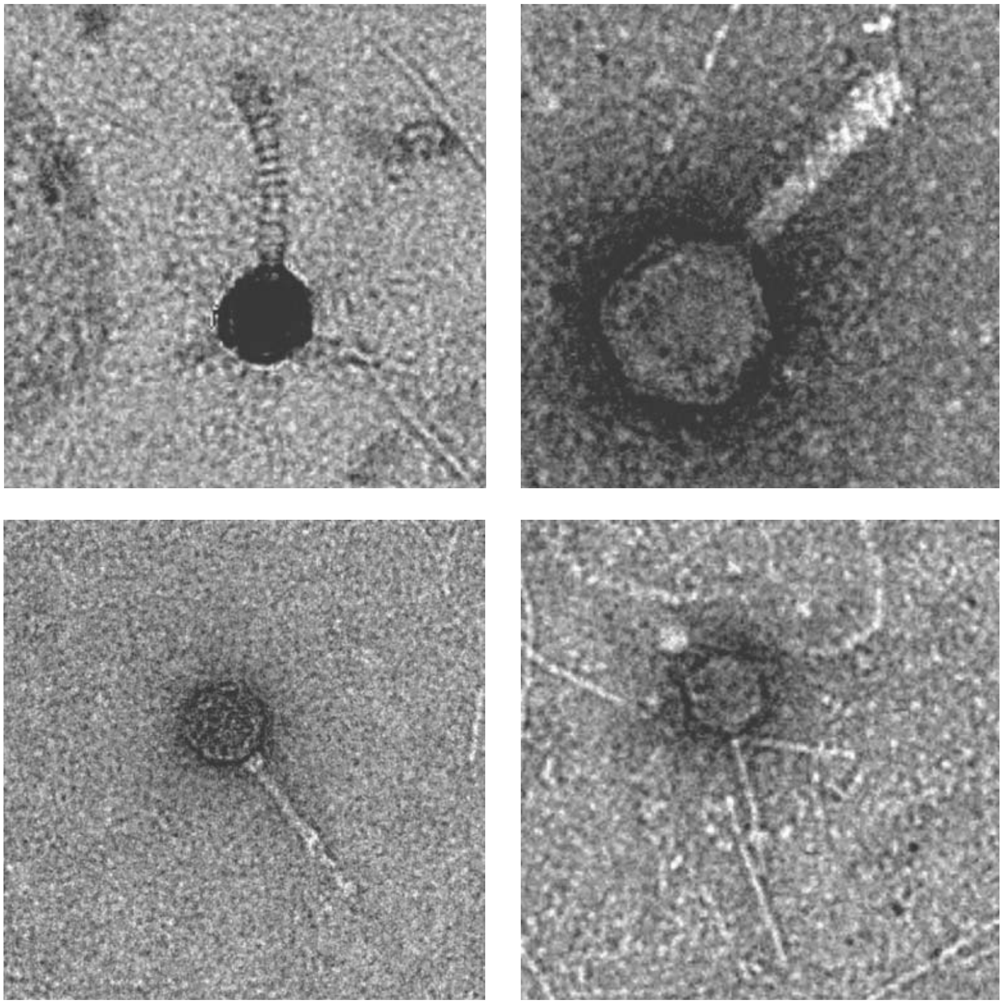


FIGURE 5.1 Some of the different types of bacteriophages, viruses that infect bacteria, found in a seawater sample taken from the Southern California coast. Bacteriophages, or phages, are found everywhere but are particularly common in seawater.

Viruses are also responsible for diseases affecting marine life other than microbes. Some viruses affect shellfish of commercial importance, while others cause serious diseases in fishes, sea turtles, and marine mammals. Humans are also vulnerable. Oysters and mussels that filter hepatitis viruses from sewage-contaminated water commonly infect humans eating raw or improperly cooked shellfish.

PROKARYOTES

Prokaryotes are the smallest and structurally simplest true living organisms and the oldest forms of life on earth. Nonetheless, they carry out nearly all the chemical processes performed by supposedly more complex organisms, as well as many that are unique to prokaryotes (Table 5.1). Most of these chemical processes actually evolved first among prokaryotes.

In contrast to viruses, prokaryotes are made up of cells. Prokaryotic cells are enclosed by a protective **cell wall.** The **cell,** or **plasma, membrane,** lies immediately inside the cell wall (see Fig. 4.7). Prokaryotes not only lack a nucleus and most other membrane-bound organelles but also differ from **eukaryotes** in the circular shape of the DNA molecules that encode their genetic information, the size of their ribosomes, and a number of other ways.

Despite their similarities, the two prokaryotic domains, **Bacteria** and **Archaea,** also have important differences, including the chemistry of their cell walls (see Table 5.2, p. 100), cell membranes, and the cellular machinery that manufactures proteins. In fact, genetic analyses indicate that bacteria and archaea are as different from each other as they are from humans.

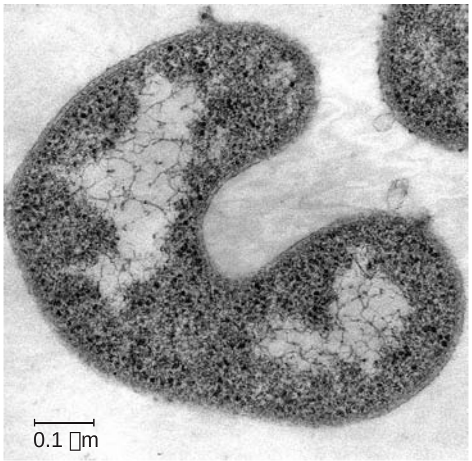
Bacteria

Bacteria (domain **Bacteria**) appear to have branched out very early on the tree of life and are genetically distant from both archaea and eukaryotes. Because they are structurally simple, bacteria (singular, **bacterium**) are classified as prokaryotes. Nevertheless, they have evolved a great range of metabolic abilities. They are abundant in all parts of the ocean.

Bacterial cells have many shapes, including spheres, spirals, rods, and rings (Fig. 5.2), depending on the species. The unique chemistry of bacterial cell walls (see Table 5.2, p. 100) makes them rigid and strong. A stiff or slimy covering often surrounds the cell wall as additional protection or a means of attaching to surfaces. The cells are very small (see Appendix A for relative size), much smaller than those of single-celled eukaryotes. About 250,000 average bacterial cells would fit on the period at the end of this sentence. There are exceptions, however, such as a sediment bacterium discovered off southwest Africa, with cells as wide as 0.75 mm (0.03 in.), large enough to be seen with the naked eye (Fig. 5.3). Another giant bacterium (0.57 mm, or 0.02 in., long) is found inside the intestines of coral reef fishes. In large numbers, marine bacteria are sometimes visible as whitish hairs on rotting seaweed or iridescent or pink patches on the surface of stagnant pools in mudflats and salt marshes.

Bacteria can grow to extremely high numbers in favorable environments such as **detritus. Decay bacteria** break down waste products and dead organic matter and release nutrients into the environment. They are vital to life on earth because

FIGURE 5.2 A high-magnification photograph taken with an electron microscope showing *Cyclobacterium marinus,* a ring-forming marine bacterium.



Nucleic Acids DNA and RNA, complex molecules that store and transmit genetic information.
Gene A sequence of *nucleotides* in the DNA molecule that directs the production of a particular protein.
Genome The complete genetic information contained in the DNA of an organism.
- Chapter 4, p. 65

Plankton Primary producers *(phytoplankton)* and consumers *(zooplankton)* that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Prokaryotes Organisms with cells that do not have a nucleus or most other organelles.
- Chapter 4, p. 69; Figure 4.7

Eukaryotes Organisms with cells that contain a nucleus and other organelles that are enclosed by membranes.
- Chapter 4, p. 69; Figure 4.8

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

FIGURE 5.3 Three cells of *Thiomargarita namibiensis,* the largest known bacterium. Cells can be 0.75 mm (0.03 in.) wide. The round, yellowish structures are sulfur granules. *Thiomargarita* lives in oxygen-poor water.

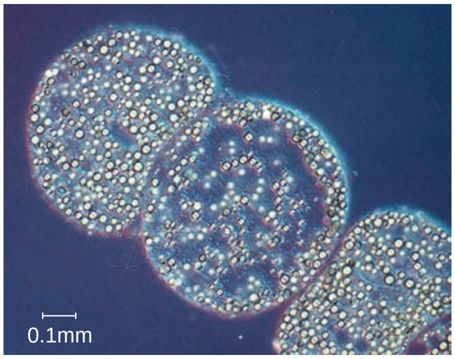


Table 5.1 Examples of Metabolic Reactions in Marine Prokaryotes

Name of Reaction	Energy Source	Other Raw Materials	By-product(s)	Production of Organic Carbon	Major Groups	Comments
Photosynthesis	Light	Carbon dioxide, water	Oxygen	Yes	Cyanobacteria	*Light captured by chlorophyll, essentially the same process performed by algae and plants*
	Light	Hydrogen sulfide	Sulfur or sulfate	Yes	Purple and green bacteria	*Light captured by bacteriochlorophyll*
Chemosynthesis						*Energy supplied by a variety of inorganic molecules, of which only few examples are included here*
Sulfur oxidation	Hydrogen sulfide	Oxygen	Sulfate	Yes	Sulfur-oxidizing bacteria	*Bacteria in wetland sediments, mudflats, deep-sea hydrothermal vents*
Aerobic ammonium oxidation	Ammonium	Oxygen	Nitrite	Yes	Nitrifying bacteria and archaea	*Bacteria in wetland sediments, mudflats, deep-sea hydrothermal vents; open-water archaea*
Nitrite oxidation	Nitrite	Oxygen	Nitrate	Yes	Nitrifying bacteria	*Bacteria in wetland sediments, mudflats, deep-sea hydrothermal vents*
Iron oxidation	Reduced iron	Oxygen	Oxidized iron	Yes	Iron-oxidizing bacteria	*Bacteria in sediments, deep-sea hydrothermal vents*
Aerobic respiration	Organic matter	Oxygen	Carbon dioxide, water	No	Heterotrophic, aerobic bacteria and archaea; decay bacteria and archaea	*Organic matter broken down using oxygen to release energy*
Anaerobic respiration						*Organic matter broken down in the absence of oxygen to release energy; less efficient than aerobic respiration*
Sulfate reduction	Organic matter	Sulfate	Hydrogen sulfide	No	Sulfate-reducing bacteria and archaea	
Nitrate reduction, denitrification	Organic matter	Nitrate, nitrite	Nitrogen gas, ammonia	No	Denitrifying bacteria	
Methanogenesis	Organic matter	Hydrogen, carbon dioxide	Methane	No	Methanogens	*Archaea in many environments*
Nitrogen fixation	ATP	Nitrogen gas	Ammonium	No	Nitrogen-fixing bacteria and archaea	*Ammonium and other compounds produced from ammonium can be used as nutrients by primary producers.*
Anaerobic ammonium oxidation (anammox reaction)	Ammonium	Nitrite	Nitrogen gas	No	Anammox bacteria and archaea	*Ammonium converted to nitrogen in the absence of oxygen to release energy*
Light-mediated ATP synthesis	Light		ATP	No	Archaeum in highly saline pools	*Light captured by bacteriorhodopsin*

they ensure the recycling of essential nutrients, as in the recycling of dissolved organic matter in oceanic food webs (see "The Microbial Loop," p. 344). Most organic matter is sooner or later decomposed, though in very deep, cold water the process is slower than elsewhere (see "Bacteria in the Deep Sea," p. 373). Decay and other types of bacteria play another crucial role because they constitute a major part of the organic matter that feeds countless bottom-dwelling animals. Even many organic particles in the water column are composed mostly of bacteria. Some marine bacteria are also involved in degrading oil and other toxic pollutants that find their way into the environment. The same process of decomposition is unfortunately involved in the spoilage of valuable fish and shellfish catches. Other types of marine bacteria cause diseases in marine animals and humans.

Bacteria are found everywhere in the marine environment, on almost all surfaces and in the water column. In fact, the most abundant forms of life on the planet seem to be bacteria, found in surprisingly high numbers in open water. Their role, though probably highly significant due to their vast numbers, remains unknown. Bacteria have also been found in seemingly harsh environments, such as in sediment 300 m (980 ft) under the floor of the Pacific Ocean.

Bacteria are structurally simple microorganisms that are particularly significant as decomposers, breaking down organic compounds into nutrients that can be used by other organisms, and as primary producers. They are also an important food source.

Cyanobacteria, once known as blue-green algae, are a group of **photosynthetic** bacteria (see "Autotrophs," p. 91). In addition to having chlorophyll *a,* as do eukaryotic photosynthetic organisms, most contain a bluish pigment called **phycocyanin.** Most marine cyanobacteria also have a reddish pigment, **phycoerythrin.** The visible color of the organism depends on the relative amounts of the two pigments. When phycocyanin predominates, the bacteria appear blue-green; when phycoerythrin predominates, they appear red.

Cyanobacteria were among the first photosynthetic organisms on earth. They are thought to have had an important role in the accumulation of oxygen (O_2) in our atmosphere. Fossil **stromatolites,** massive **calcareous** mounds formed by cyanobacteria, are known to date back some 3 billion years. Stromatolites are still being formed in tropical seas (Fig. 5.4).

Cyanobacteria are widely distributed in the marine environment. *Prochlorococcus,* a minute cyanobacterium, is thought to be the most abundant photosynthetic organism in the ocean. It is particularly common in tropical and subtropical waters. Many species can tolerate wide ranges of salinity and temperature, while others are found in unexpected places, like inside the hair of polar bears! Some cyanobacteria, called **endolithic,** burrow into calcareous rocks and coral skeletons. Others form thick, dark crusts along the wave-splashed zone of rocky coasts. Some exploit oxygen-poor sediments, which may include polluted sites. **Planktonic** species may rapidly multiply and change the color of the water. Some so-called **red tides** (see "Red Tides and Harmful Algal Blooms," p. 334) are caused by cyanobacteria that contain a red pigment. A few species can cause skin rashes on swimmers and divers.

Some cyanobacteria live on the surface of seaweeds and seagrasses. Photosynthetic organisms that live on algae or plants are called **epiphytes.** Some biologists, however, use this term to refer to *all* organisms living on algae or plants. Other cyanobacteria live inside algae and are called **endophytes.**

Cyanobacteria are photosynthetic bacteria. They were one of the first groups of photosynthetic organisms on earth.

Archaea

Archaea (domain **Archaea**) are among the simplest, most primitive forms of life. Some look very similar to the oldest fossils ever found, cells estimated to be at least 3.8 billion years old. Archaea are thought to have had an important role in the early evolution of life. Like bacteria, their cells are small and may be

Calcareous Made of calcium carbonate ($CaCO_3$).
- Chapter 2, p. 32

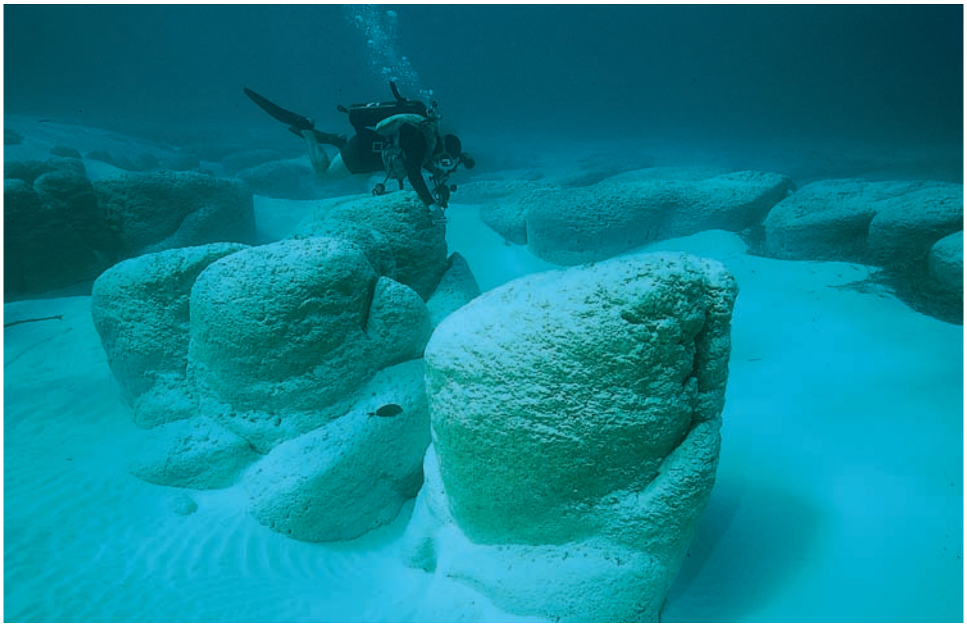


FIGURE 5.4 Stromatolites, calcareous mounds deposited by cyanobacteria, are frequently found as fossils. These, however, are living stromatolites growing in shallow water in the Exuma Cays, Bahama Islands.

EVOLUTIONARY PERSPECTIVE

Symbiotic Bacteria—the Essential Guests

Some bacteria have evolved to live in close, or **symbiotic,** associations with other marine organisms. Some symbiotic bacteria are **parasites** that may cause a disease. Others, on the other hand, benefit their hosts. These symbiotic bacteria began their association by increasing the chances of survival of the host and evolved to become essential—hosts could not survive without them. In many cases the symbiotic bacteria are even sheltered in special tissues or organs that evolved in the host, an example of **coevolution,** in which two species evolve in response to each other.

All eukaryotic organisms, including humans, shelter bacteria without which they could not live. The chloroplasts and mitochondria of eukaryotic cells evolved from symbiotic bacteria (see "From Snack to Servant: How Complex Cells Arose," p. 73). These bacteria have become an integral part of all complex cells.

There are many cases of symbiotic bacteria among marine organisms. Symbiotic bacteria, for example, are involved in digesting the wood that is ingested by shipworms *(Teredo),* which happen to be bivalve molluscs, not worms. Like all wood-eating animals, shipworms lack cellulase, the enzyme needed to digest cellulose, the main component of wood. Wood is a surprisingly common habitat in many marine environments, so everything from driftwood to boat bottoms is exploited by shipworms, thanks to their symbiotic bacteria.

Symbiotic bacteria are also responsible for the light, or **bioluminescence,** that is produced by some fishes, squids, octopuses, and other animals of the deep (see "Bioluminescence," p. 365). The bacteria are usually sheltered in special light-producing organs, or **photophores.** These deep-sea animals, which live in darkness, use light to communicate with other members of their species, lure prey, blend with the light that filters from the surface, and perform other functions. Flashlight fishes *(Anomalops),* which live in shallow tropical waters, lodge their symbiotic bacteria in an organ beneath each eye. A shutter mechanism controls the emission of light, so that the fish can "blink" at night. Groups of fish blink in synchrony, a behavior that is involved in attracting prey.

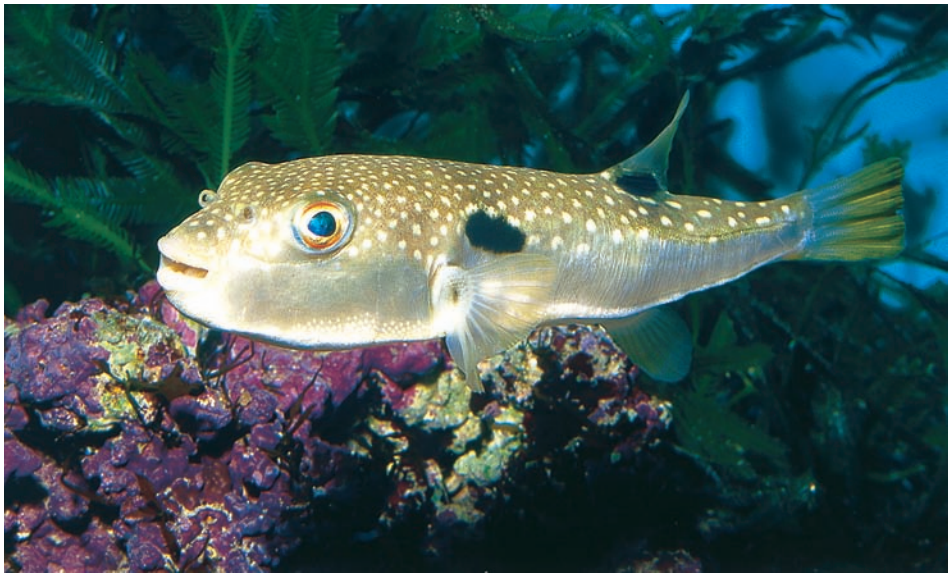
Chemosynthetic bacteria symbiotic with mussels, clams, and tubeworms that live around deep-sea hydrothermal vents have a very particular role: manufacturing organic matter from CO_2 and the abundant hydrogen sulfide (H_2S) from the vents. The symbiotic bacteria live in a special organ, the feeding body, of the giant hydrothermal-vent tubeworm *Riftia* (see Fig. 16.29).

Marine symbiotic bacteria can also affect human health. Pufferfishes store a toxin that is deadly to any predators (including humans) that eat them. The fish, or *fugu,* is a delicacy in Japan. Licensed chefs must prepare the fish; otherwise, the toxin **(tetrodotoxin)** will kill anyone feasting on fish that has been improperly prepared. Tetrodotoxin is a deadly neurotoxin (that is, it affects the nervous system). In fact, it is one of the most powerful poisons known, and there is no antidote. The deadly toxin is stored mostly in the liver and gonads of the fish, so the internal organs must be expertly removed. Mistakes do happen and numerous deaths (including the suicides of disgraced cooks) take place every year in Japan. Cooks may still be guilty, but not the puffers: the toxin is now known to be produced not by the fish but by symbiotic bacteria. No one knows yet how the fish is immune to the bacterial toxins.

Tetrodotoxin and very similar toxins have also been found in a variety of marine organisms, including flatworms, snails, crabs, sea stars, and several species of fishes. It has also been found in the blue-ringed octopuses, notoriously toxic animals. Tetrodotoxin of an unknown source has also been found in dead sea urchins and is suspected as their cause of death. We are not yet sure if in all these animals the toxin is produced, as in *fugu,* by symbiotic bacteria or if it is accumulated from their food. In arrow worms, however, symbiotic bacteria in the mouth do produce tetrodotoxin that is used to paralyze prey.

Being a neurotoxin, tetrodotoxin may block pain signals in humans. A derivative being tested as a pain reliever for cancer and other diseases would have the advantage of not being addictive, as are morphine and similar drugs.

The production of powerful toxins that are used by other organisms is just one example of the amazing abilities of bacteria—invisible to the eye but powerful giants when it comes to their role in the environment.



A Japanese pufferfish, or *fugu (Takifugu niphobles).*

spherical (Fig. 5.5), spiral, or rod-shaped. In fact, until recently archaea (singular, **archaeum**) were thought to be bacteria. Despite being prokaryotic, however, there is evidence that archaea are more closely related to eukaryotes than to bacteria.

Some groups of archaea were discovered only recently, first in extreme environments on land, such as hot sulfur springs, saline lakes, and highly acidic or alkaline environments. Archaea were thus named "extremophiles," meaning "lovers of extremes." Archaea were subsequently found in extreme marine environments, such as in very deep water, where they survive at pressures of 300 to 800 atmospheres. Some archaea live at the high temperatures of **hydrothermal vents** (Fig. 5.5). Some of these cannot grow in temperatures less than 70° to 80°C (158° to 176°F), and one hydrothermal vent archaeum can live at 121°C (250°F), the highest of any known organism. Other archaea depend on extremely salty environments, such as coastal salt pans and deep ocean basins (see "Prokaryotes of Deep Hypersaline Basins," p. 93). Others are found in highly acid or alkaline conditions.

Because the first groups of microorganisms to be classified as archaea were extremophiles, it was thought that *all* archaea were extremophiles; indeed, the two terms became almost synonymous. New techniques based on detecting **nucleic acid** sequences, however, have shown that archaea are common in many marine environments, not only in the water column (see "Tiny Cells, Big Surprises," p. 92) but in sediments as well. Some archaea are also known to live symbiotically in sponges, sea cucumbers, and fishes. Thus, the **hypothesis** that archaea are restricted to extreme environments was proven false.

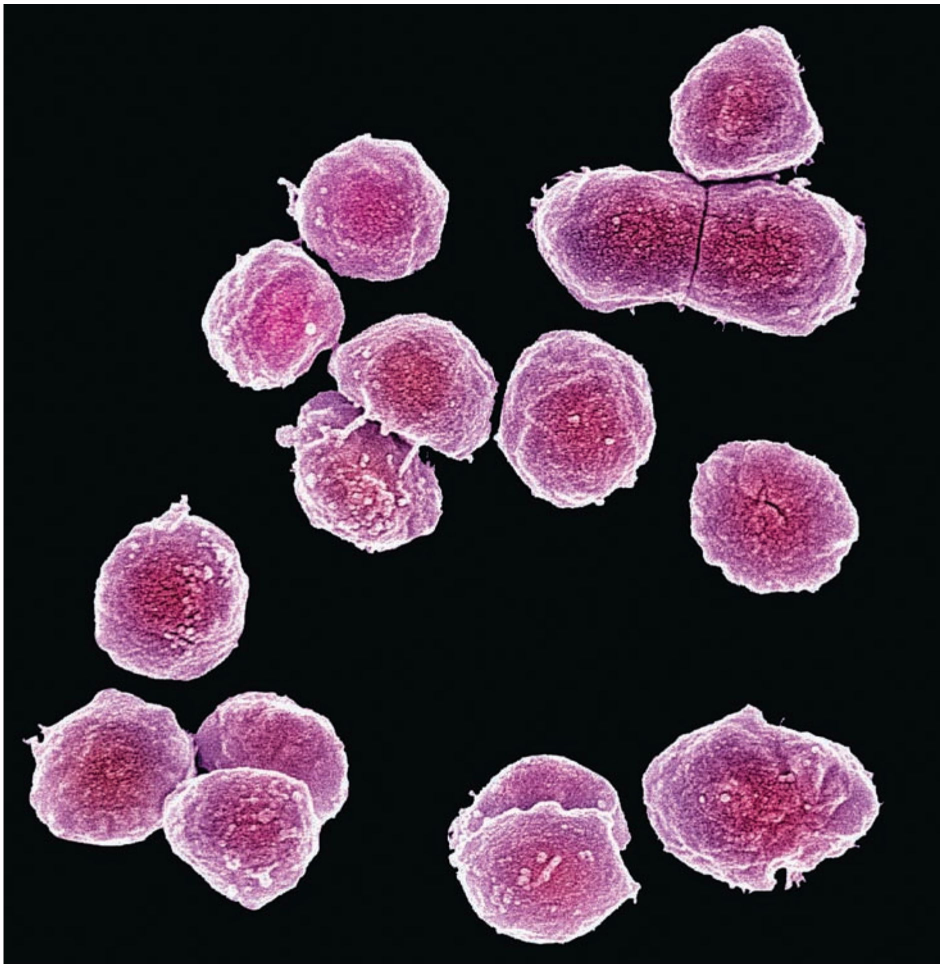


FIGURE 5.5 *Methanocaldococcus jannaschii* is a methane-producing archaeon that lives at high temperatures near deep-sea hydrothermal vents. It was the first archaeon to have its genome sequenced.

> Archaea are prokaryotic microorganisms once thought to be bacteria but more closely related to eukaryotes. They were first known from extreme environments, but they are now known to be common in the marine environment.

Prokaryote Metabolism

Prokaryotes show an amazing variety of chemical reactions that are involved in the transfer of energy and in the manufacture of chemical compounds. Some actually obtain energy in more than one way. **Metabolism** is all the chemical reactions that take place in an organism.

Autotrophs **Autotrophic** bacteria and archaea make their own organic compounds and thus are primary producers. Energy sources vary. Some autotrophic bacteria, such as the cyanobacteria previously mentioned, are photosynthetic or **photoautotrophic.** They contain chlorophyll or other photosynthetic pigments (see Table 5.2, p. 100) to trap light energy to manufacture organic compounds from carbon dioxide (CO_2); cyanobacteria release oxygen in the process (see Table 5.1). Photosynthesis takes place on folded membranes within the bacterial cell (see Fig. 4.7 and photo on p. 73) rather than in chloroplasts, as in algae and plants.

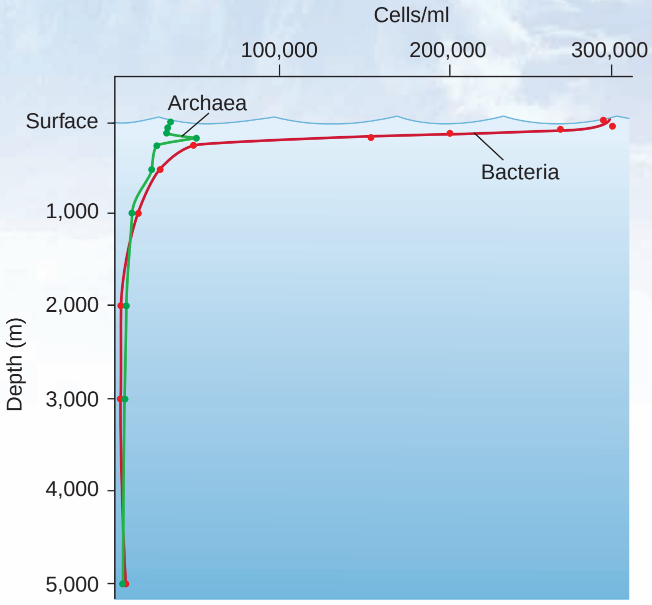
Photosynthetic bacteria account for much of the primary production in many open-ocean areas. Even bacteria living at depths where no surface light penetrates have been suggested as using the faint glow of hydrothermal vents to perform photosynthesis. Though the end products may be similar, the biochemistry of bacterial photosynthesis is different from that of algae and plants. It also varies considerably among different

Hydrothermal Vents Undersea hot springs associated with mid-ocean ridges and other geologically active environments.
- Chapter 2, p. 37

Hypothesis A statement about the world that might be true.
- Chapter 1, p. 12

Autotrophs Organisms that can use energy (usually solar energy) to make organic matter.
- Chapter 4, p. 67

Tiny Cells, Big Surprises



Depth distribution of bacteria and archaea in the subtropical North Pacific.

It is surprising how little biologists know about the lives of marine microbes. We know they are everywhere but we are not sure how many types there are, how common they are, and what exactly they are up to. The situation is rapidly changing as we apply new techniques and approaches to studying the private lives of marine microorganisms that call the ocean home.

Information about marine microbes (what nutrients the microbes need to grow, the type of compounds they produce, and such) has traditionally been gathered mostly from organisms collected in water samples and then grown under artificial conditions. Many organisms, unfortunately, do not grow in the lab, and their presence in samples goes undetected. At least some of this information has been used by marine ecologists to deduce the role of microbes in the big ocean world—the role of decay bacteria in releasing nutrients, for example, and of bacteria that convert free nitrogen into nitrates or make dissolved organic matter (DOM) available to larger forms of life. Still, bacteria and other marine microbes are poorly understood. Some groups of microbes remained undiscovered for a long time. Most archaea, for instance, have been known only since the 1970s.

Viruses and the minute prokaryotic cells of bacteria and archaea and the smallest eukaryotic cells of some algae and other organisms seem to be everywhere but are very difficult to collect and characterize by the microscopic examination of cells. Instead of culturing or filtering out these cells, fragments of nucleic acid (see "Nucleic Acids," p. 65) are collected from the water and **sequenced.** The presence of organisms can be detected by identifying characteristic DNA or RNA sequences. Furthermore, the partial sequences can yield information about the unique characteristics of these microbes, even if whole cells or whole nucleic acid molecules are not collected.

The presence of RNA sequences characteristic of archaea in seawater and sediment samples has shown archaea to be abundant. In 2001 two groups of archaea were found to be extremely abundant in water samples collected from depths below the photic zone—that is, where light does not penetrate (see Chapter 16). The samples, collected from the Pacific Ocean south of Hawai'i, showed that archaea were rare at the surface but sharply increased in abundance below depths of 250 m (720 ft). Below 1,000 m (3,280 ft) archaea were as common as bacteria. Judging from their numbers and the huge volume of the ocean in question, these archaea are among the ocean's most abundant forms of life. DNA sequences in samples from the Sargasso Sea have demonstrated the presence of at least 1,800, and possibly as many as 50,000, new species of microbes.

Similar techniques based on the detection of characteristic nucleic acid sequences have been used to identify previously unknown eukaryotic microorganisms. These eukaryotes are larger than prokaryotes but still minute (smaller than 2 to 3 μm), making them difficult to collect and study. This sharply contrasts with other unicellular but larger eukaryotes in the plankton, which are relatively easy to collect using plankton nets (see "The Plankton: A New Understanding," p. 329). In 2001 two new groups related to dinoflagellates were discovered at depths of 250 to 3,000 m (720 to 9,840 ft) near Antarctica. Similar but unique groups of eukaryotic microorganisms (including yet another new group related to dinoflagellates) were reported at the same time by another team working at depths of 75 m (246 ft) in the tropical Pacific. The fact that some of these microorganisms, collected in relatively shallow water where light still penetrates, are photosynthetic, adds a new dimension to the discovery. They represent a previously unknown source of primary production in typically unproductive tropical waters. Other groups of minute algae have been discovered in recent years, including three groups that are related to dinoflagellates. Other groups certainly remain to be discovered.

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groups of bacteria. Some photosynthetic bacteria, for example, have a kind of chlorophyll unique to prokaryotes and produce sulfur (S) instead of oxygen (see Table 5.1). It is thought that some bacteria may use a pigment called proteorhodopsin to capture light energy and store it in **ATP.** They do not have chlorophyll or use the energy to manufacture organic compounds from carbon dioxide and thus are not photosynthetic. An archaeum *(Halobacterium)* similarly lacks chlorophyll but contains a pigment, bacteriorhodopsin, that converts light energy directly into ATP. Marine microbes can therefore use light as an energy source in many ways, not just in photosynthesis.

Other bacterial autotrophs, called **chemosynthetic,** or **chemoautotrophic,** derive energy not from light but from chemical compounds, including **hydrogen sulfide (H_2S)** and other sulfur, nitrogen, and iron compounds (see Table 5.1). Some chemosynthetic archaea, the methanogens, produce methane (CH_4). One example is *Methanopyrus,* an archaeum that has been isolated from sediments near hydrothermal vents.

Prokaryotes show a wide variety of metabolic processes. Many bacteria (including cyanobacteria) and some archaea are autotrophs and account for much of the oceanic primary production.

EYE ON SCIENCE

Prokaryotes of Deep Hypersaline Basins

An international team of marine biologists recently used DNA and RNA sequencing (see "Tiny Cells, Big Surprises," p. 92) to detect a variety of bacteria and archaea in one of the most inhospitable marine environments known, deep pockets of water called hypersaline basins because of their very high salt concentrations. Another extreme condition in these basins is that the water contains no oxygen.

At least four of these basins are present in the eastern Mediterranean Sea. They probably formed when tectonic activity (see "Sea-Floor Spreading and Plate Tectonics," p. 27) exposed subterranean salt deposits to seawater and the deposits dissolved. The deposits were formed several million years ago but the actual basins were formed more recently, perhaps a few thousand years ago. The salinity of the water averages 10 times that of normal seawater, much higher than most organisms can tolerate. The water also contains various ions in concentrations that are usually harmful to life—the chloride content at one basin is 18 times that of normal seawater, magnesium almost 100 times higher.

High salinity means high density, so the hypersaline water remains on the bottom, isolated from the less dense water above. No oxygen is produced by photosynthesis because light is absent at the great depths, and little oxygen enters the water mass from the water above.

Many different bacteria and archaea have evolved in these basins, which are isolated not only from the rest of the water column but also from each other. As a result, each basin contains a unique combination of microbes. Both bacteria and archaea are present in all four basins but bacteria dominate in three of them, while archaea are more common in the other. Prokaryotes identified so far include sulfate reducers, methanogens, and anaerobic heterotrophs (see Table 5.1). Though the water in the basins is highly isolated, methane gas and some sulfur compounds may find their way into the water above.

Studying the prokaryotic life of these basins is of great interest because scientists hypothesize that the earliest forms of life on earth were prokaryotes that lived in hypersaline water. These studies thus give clues of what to expect if life is found in extraterrestrial environments, some of which may resemble hypersaline basins here on earth.

Research on the prokaryotes of hypersaline basins continues in several European laboratories. Teams are analyzing the genome of these microbes, looking for genes that code for unusual proteins. Scientists have already discovered an enzyme that is unusually tolerant of high salt concentrations and pressure. Researchers are also interested in finding out what might grow under high magnesium concentrations, an environment recently discovered on Mars and Europa, one of Jupiter's moons.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

Heterotrophs Most marine bacteria, like animals, are **heterotrophs** that obtain energy from organic matter by **respiration** (see Table 5.1). Many heterotrophic bacteria and archaea are decomposers. Respiration in **aerobic** bacteria and archaea uses oxygen, as in most other groups of organisms, whereas in **anaerobic** species respiration does not require oxygen. Anaerobic bacteria do not grow when oxygen is present and thrive when it is absent, as in sediments that are devoid of oxygen, or **anoxic.** This is the case in bacteria that use sulfate (SO_4^{-2}) instead of oxygen to perform respiration, producing in the process the hydrogen sulfide (H_2S) that is to blame for the rotten-egg smell of some sediments (see Fig. 11.29).

Heterotrophic prokaryotes obtain energy from organic matter. Many are decomposers.

Nitrogen Fixation Many planktonic cyanobacteria (such as *Trichodesmium*) carry out **nitrogen fixation,** converting gaseous nitrogen (N_2) into ammonium (NH_4^{+1}), which, like nitrate (NO_3^{-1}) and other nitrogen compounds into which most of the ammonium is transformed (see Table 5.1), can be used as a nitrogen source by primary producers (see "Cycles of Essential Nutrients," p. 226). Other bacteria and some archaea are also known to be nitrogen fixers. Nitrogen fixation requires energy, which is provided by ATP generated from photosynthesis or other reactions.

Some prokaryotes, particularly cyanobacteria, are nitrogen fixers. They convert gaseous nitrogen into ammonium, which is used by primary producers.

UNICELLULAR ALGAE

Algae (singular, **alga**) are a very diverse group of simple, mostly aquatic (that is, marine and freshwater), mostly photosynthetic organisms. Being eukaryotic, their cells contain a nucleus and other organelles enclosed by membranes. Photosynthesis takes place in **chloroplasts**—green, brown, or red organelles with layers of internal membranes that contain photosynthetic pigments (see Fig. 4.8*b*). The color of algae is a result of the pigments and their

ATP The molecule used to store and transfer energy in metabolic reactions.
- Chapter 4, p. 66

Heterotrophs Organisms that cannot make their own food and must use the organic matter produced by autotrophs.
- Chapter 4, p. 67

concentration. In contrast to the land plants with which we are familiar, algae lack flowers and have relatively simple reproductive structures. Their nonreproductive cells are also mostly simple and unspecialized. Algae lack true leaves, stems, and roots.

Biologists used to refer to algae as plants. Many of the unicellular algae, however, show animal-like characteristics. Some swim by moving their flagella, and distinguishing these free-swimming algae from some of the structurally simpler animals can be difficult at first glance. Some species carry out photosynthesis as plants do, and very similar species move and eat food particles as animals do. Some species do both and are claimed by both botanists (plant biologists) and zoologists (animal biologists). These unicellular organisms are collectively called protists for convenience, although most biologists no longer consider the traditional kingdom **Protista** to be a separate kingdom because various groups of protists have different evolutionary histories. Multicellular seaweeds are also considered to be protists, mostly because they lack the specialized tissues of plants. Seaweeds, together with other multicellular primary producers, the marine plants, are discussed in Chapter 6.

Algae are protists. They are mostly aquatic primary producers that lack the specialized tissues of plants. They range in size and complexity from single cells to large, multicellular seaweeds.

Diatoms

Diatoms (division, or phylum, **Bacillariophyta**) are unicellular, though many species aggregate into chains or star-like groups. Diatom cells are enclosed by cell walls made largely of **silica (SiO_2),** a glass-like material. This glassy shell, or **frustule,** consists of two tightly fitting halves often resembling a flat, round, or elongated box (Fig. 5.6). The frustule typically has intricate perforations and ornaments such as spines or ribs, making diatoms strikingly beautiful when seen under a microscope. The frustule allows light to pass through, so that the conspicuous golden brown chloroplasts can capture light energy for photosynthesis. The minute perforations allow dissolved gases and nutrients to enter and exit. The sinking of open-ocean diatoms below the well-lit surface layer is often slowed by oil droplets in their cells and spines on the frustules (see "Staying Afloat," p. 337).

The characteristic color of diatoms is due to yellow and brown **carotenoid** pigments, in addition to two types of chlorophyll, *a* and *c*. Diatoms are efficient photosynthetic factories, producing much-needed food (the food being the diatoms themselves), as well as oxygen, for other forms of life. Diatoms are very important open-water primary producers in temperate and polar regions (see Table 15.1, p. 332; "Epipelagic Food Webs," p. 343). In fact, the huge number of diatom cells in the ocean account for a hefty share of the organic carbon and oxygen produced on planet earth.

Around half the estimated 12,000 living species of diatoms are marine. Most are planktonic, but many produce a stalk-like structure for attachment to rocks and other surfaces in shallow water, where they contribute significantly to primary production. The brownish scum sometimes seen on mudflats or glass aquaria often consists of millions of diatom cells. Some are able to glide slowly on surfaces. A few are colorless, having no chlorophyll, and live as heterotrophs on the surfaces of seaweeds. Some planktonic diatoms produce a potent toxin, **domoic acid,** which accumulates in shellfish and plankton-feeding fishes that eat the diatoms. The toxin causes a serious, sometimes fatal, illness of the nervous system in humans and marine mammals that eat contaminated shellfish or fish.

Diatoms are unicellular organisms that live mostly as part of the plankton. A silica shell is their most distinctive feature. They are important open-water primary producers in cold waters.

Diatoms reproduce mostly by cell division, a type of **asexual reproduction.** The overlapping halves of the frustule separate, and each secretes a new, smaller half. The smaller, lower frustule of the parent cell becomes the larger frustule of a daughter cell, which then secretes a new, smaller frustule (Fig. 5.7). Full size may be regained by the development of resistant stages known as **auxospores.** Auxospores eventually give rise to larger cells that display the frustule characteristic of the species.

Favorable environmental conditions, such as adequate nutrients and light, trigger periods of rapid reproduction called **blooms.** This is a general phenomenon that also occurs in other algae.

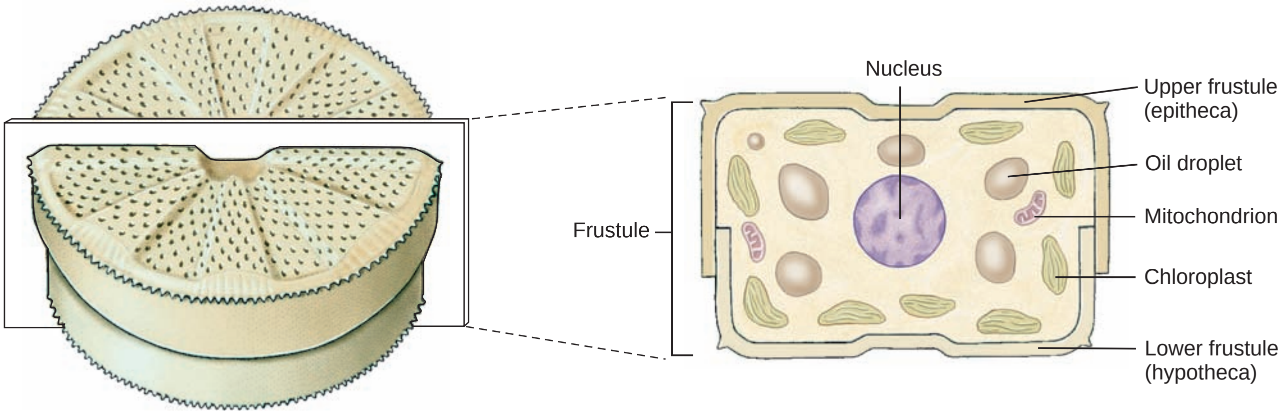

FIGURE 5.6 Diagrammatic representation of a diatom cell (also see Fig. 15.3).

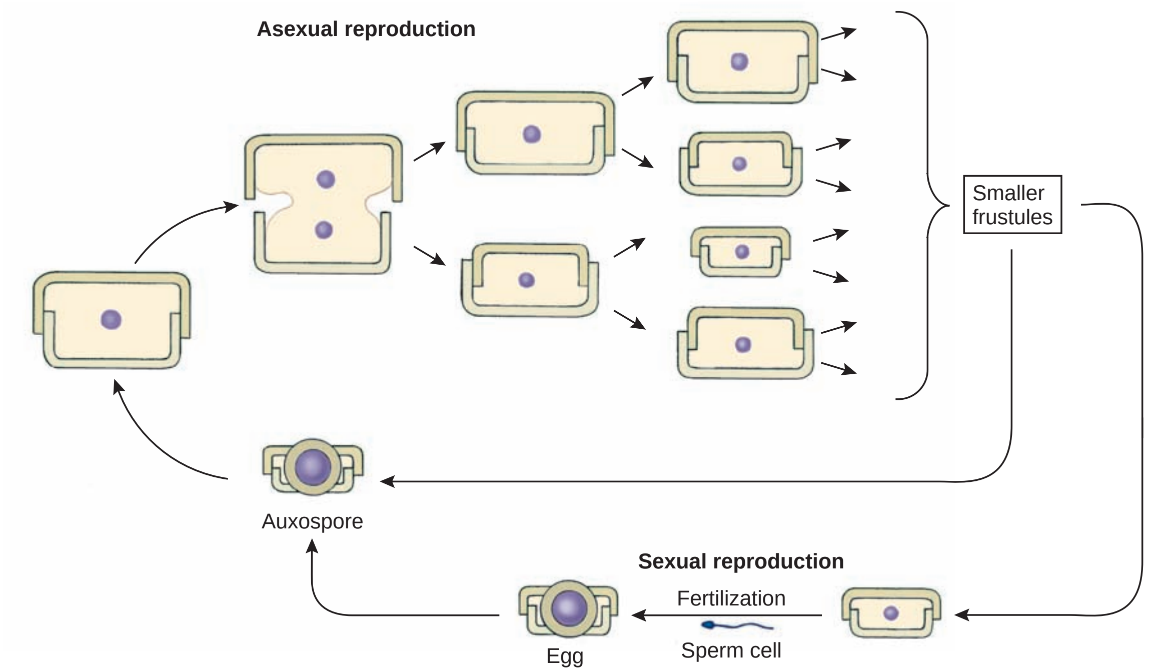

FIGURE 5.7 The usual method of reproduction in diatoms is by cell division. Most, but not all, frustules get smaller after each successive division. Resistant cells called auxospores are produced two ways: directly from the expansion of a smaller frustule or by sexual reproduction when an egg is fertilized by a sperm cell, both of which are liberated from separate frustules.

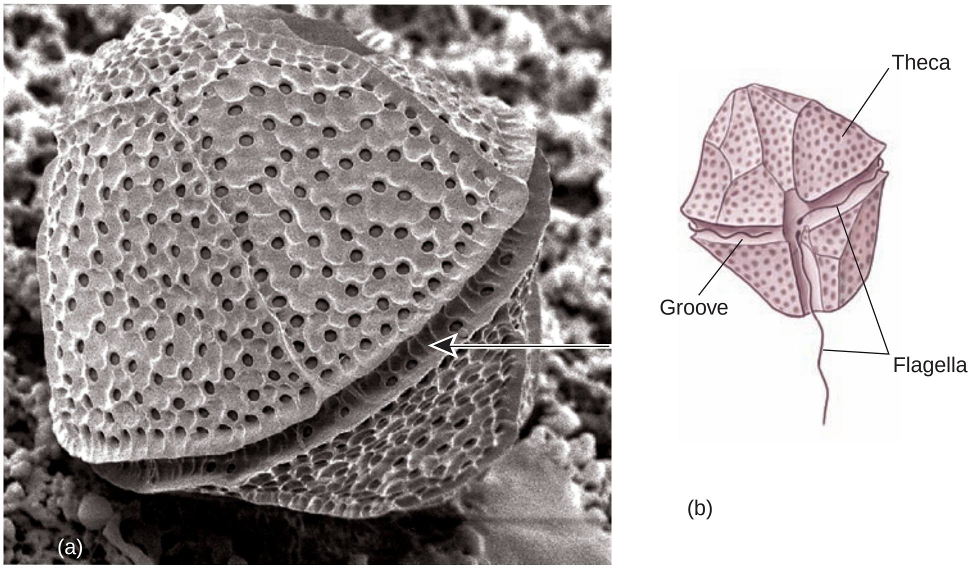

FIGURE 5.8 Dinoflagellates like *Gonyaulax polyedra* have a cell wall, or theca, which consists of cellulose plates. The theca is marked by grooves for the flagella; only one groove is visible here (arrow). This species is bioluminescent and it produces red tides.

During blooms most diatoms get progressively smaller, not only because of asexual reproduction but also as a result of depletion of silicate from the water by the growing population.

The glassy frustules of dead diatoms eventually settle to the bottom of the sea floor. Here they may form thick deposits of siliceous material that cover large portions of the ocean floor. Such **biogenous sediments** are known as **diatomaceous ooze,** a type of **siliceous ooze.** Huge fossil deposits of these sediments can be found inland in various parts of the world. The siliceous material, or **diatomaceous earth,** is mined and used in products such as filters for swimming pools, for clarifying beer, as temperature and sound insulators, and as mild abrasives in toothpaste.

Dinoflagellates

The **dinoflagellates** (division, or phylum, **Dinophyta**) make up another large group of planktonic, unicellular organisms. Their most outstanding characteristic is the possession of two flagella, one wrapped around a groove along the middle of the cell and one trailing free (Fig. 5.8). These flagella direct movement in any direction. Most dinoflagellates have a cell wall armored with plates made of **cellulose,** the characteristic

Types of reproduction:
Asexual (or *vegetative*) The production of new individuals by simple division (or other means) without involving *gametes*, so that the offspring are genetically identical to the parents.
Sexual The production of new individuals by the formation of *gametes* (sperm and eggs), so that the offspring are genetically different from the parents.

- Chapter 4, p. 77

The Bay of Fire

Imagine entering a quiet tropical bay at night. There are no lights on shore, and on a moonless night the spectacle is unforgettable. As the propeller of your boat churns the black water, an intense blue-green light is left behind, like an eerie trail of cool fire. Outside the bay you see a few sparks of light as you approach, but inside the bay things are very different. Long streaks of light shoot like fireworks beneath the boat. They are created by fleeing fish. A swim in the bay is even more spectacular. Your dive into the water is accompanied by a blinding flood of light, and sparks scatter out as you wave your arms.

Such light effects result from an unusual concentration of bioluminescent dinoflagellates, a natural and permanent phenomenon in a few select locations such as *Bahía Fosforescente,* or Phosphorescent Bay, in southwestern Puerto Rico.

Bioluminescent Bay might be a more apt name because the light is produced by living organisms. The bay's most important source of bioluminescence is *Pyrodinium bahamense,* a unicellular, photosynthetic dinoflagellate about 40 microns (μm; 0.004 cm, or 0.0015 in.) in diameter. As many as 720,000 individuals are found in a gallon of water, many more than outside the bay. The bay is small, about 90 acres, and fan-shaped, and it does not exceed 4.5 m (15 ft) in depth. The main reason that the dinoflagellates are concentrated there is that the bay is connected to the open sea by a narrow, shallow channel. As water containing the dinoflagellates flows into the bay, evaporation in the shallow water causes the surface water to sink because of the increase in salinity and therefore density. Evaporation is enhanced by the dry and sunny days. The *Pyrodinium* stays near the surface and is therefore not carried out as the denser water flows out along the bottom of the shallow entrance. The tidal range is only about a foot at the most, so water exchange with the outside is limited. The bay thus acts as a trap that keeps the dinoflagellates from leaving.

Bahía Fosforescente in Puerto Rico.

Of all the planktonic organisms that enter the bay, why is *Pyrodinium* favored? A key factor seems to be the thick mangrove trees bordering the bay. They grow along the muddy shores, together with all kinds of organisms living attached to their roots. Mangrove leaves fall into the water, where intense bacterial decomposition increases the organic nutrient levels in the water. Some nutrients essential to the growth of *Pyrodinium,* perhaps vitamins, may be released by bacteria or other microorganisms.

Bahía Fosforescente is protected to keep the critical natural balance intact, but bioluminescence has noticeably decreased during recent years. The same phenomenon in a bay in the Bahamas disappeared when its narrow entrance was dredged to allow larger boats, with larger loads of tourists, to pass through.

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component of the cell walls of seaweeds and land plants. The plates may have spines, pores, or other ornaments.

Though most dinoflagellates photosynthesize, many can also ingest food particles. A few have a light-sensitive pigment spot that acts as a crude eye. It has been suggested that during their evolution dinoflagellates gained the ability to function as primary producers by capturing and using chloroplasts from other algae. Almost all known dinoflagellates, around 1,200 living species, are marine. Dinoflagellates are important planktonic primary producers, especially in warm water (see Table 15.1, p. 332).

Dinoflagellates reproduce almost exclusively by simple cell division (see Fig. 4.18). They sometimes form blooms that color the water red, reddish-brown, yellow, or other unusual shades (see "Red Tides and Harmful Algal Blooms," p. 334). Some of these dinoflagellates release toxic substances, and seafood collected during red tide periods may be poisonous. Other dinoflagellates are noted for the production of light, or bioluminescence (see "The Bay of Fire," above). Though bioluminescence has also been observed in some bacteria and many types of animals, dinoflagellates are generally responsible for the diffuse bioluminescence sometimes seen on the sea surface. This effect is, of course, seen only at night. It is especially bright if the water is disturbed by a boat or when a wave crashes on the shore.

A group of round, golden brown dinoflagellates called **zooxanthellae** live in close association with a variety of animals. Animals harboring zooxanthellae range from sponges and sea anemones to giant clams. It is perhaps in reef-building corals where zooxanthellae are most significant (see Fig. 14.1). They fix carbon dioxide by photosynthesis, release organic matter used by the coral, and help in the formation of the coral skeleton (see "Coral Nutrition," p. 305).

A few highly modified dinoflagellates are parasites of seaweeds and some marine animals. Like zooxanthellae, these highly specialized forms reveal their true nature by having life cycles that include free-swimming stages resembling typical dinoflagellates.

One such dinoflagellate is *Pfiesteria,* sometimes called the "phantom dinoflagellate" because it spends most of its life as a harmless resting stage, or cyst, in the sediment. It has been suggested that coastal pollution in the form of excessive nutrients can trigger blooms of *Pfiesteria. Pfiesteria* and *Pfiesteria*-like microorganisms are responsible for deadly open sores on fishes. *Pfiesteria* causes the sores by producing a recently discovered toxin, not by actively feeding on the fishes' tissues as first thought. These parasites are also known to be harmful to crabs, oysters, and clams and have been implicated in sores and in symptoms such as temporary memory loss in humans.

Dinoflagellates are unicellular organisms that have two unequal flagella. Some are noted for their emission of light. Zooxanthellae are dinoflagellates that are symbiotic with marine animals, especially reef corals.

Other Unicellular Algae

Three additional groups may be abundant in some areas and thus very significant primary producers in the plankton (see Table 15.1, p. 332). **Silicoflagellates** (division, or phylum, **Chrysophyta**) are characterized by a star-shaped internal skeleton made of silica (Fig. 5.9) and two flagella of different lengths. Fossil silicoflagellates are common in marine sediments and can be used to date the sediments. Typical **coccolithophorids** (division, or phylum, **Haptophyta**) are flagellated, spherical cells covered with button-like, ornamented structures called **coccoliths** made of calcium carbonate (Fig. 5.10). Coccoliths can be found in sediments as fossils. **Cryptophytes** (division, or phylum, **Cryptophyta**) have two flagella and lack a skeleton. Like other eukaryotes, cryptophytes have a chloroplast derived from a prokaryote (see "From Snack to Servant: How Complex Cells Arose," p. 73), but the chloroplast is contained within a reduced eukaryotic cell that lives symbiotically inside the cryptophyte cell. Members of these three groups of algae are so small that hundreds could fit into a large diatom or dinoflagellate cell.

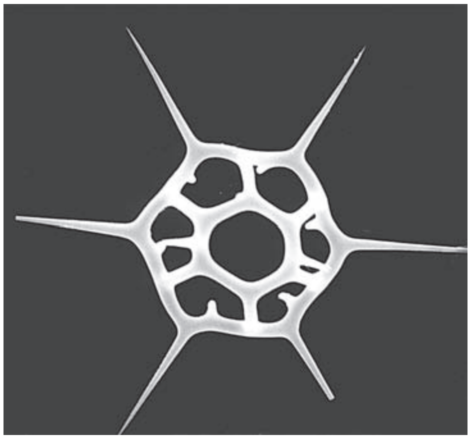


FIGURE 5.9 Skeleton of *Dictyocha speculum,* a silicoflagellate.

PROTOZOANS: THE ANIMAL-LIKE PROTISTS

Protozoans are structurally simple and very diverse eukaryotic organisms that are traditionally considered to be animal-like. Most biologists agree that protozoans (meaning "first animals") actually comprise several groups of unrelated origins. Having a single cell is about the only thing that protozoans—which show an enormous diversity in structure, function, and lifestyle—have in common. Though a few form colonies, most are single-celled, unlike true animals, and are visible only under a microscope. Like animals, protozoans are heterotrophs and ingest food. Some, however, also contain chlorophyll and photosynthesize.

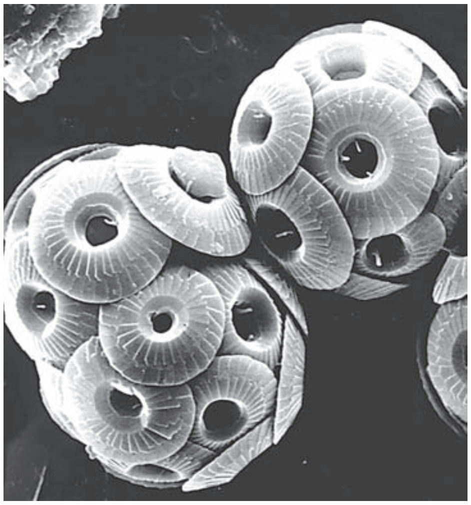


FIGURE 5.10 Coccolithophorids, such as *Umbilicosphaera sibogae* from Australia, are tiny, single-celled phytoplankton that can be significant primary producers in the open ocean. The plates that cover the cell are made of calcium carbonate.

There is considerable disagreement as to how to classify the estimated 50,000 species of protozoans, though they are generally considered to be protists along with unicellular algae and seaweeds.

> Protozoans are the most animal-like of the protists. They are eukaryotic and unicellular. They are essentially heterotrophic and ingest food, as animals do.

The minute size and apparent simplicity of protozoans disguise a complex nature. As in all unicellular organisms, each cell might be described as a "super cell" because it can perform many of the same functions carried out by the multitude of cells in structurally more complex organisms.

Protozoans inhabit water everywhere, living not only in marine and freshwater environments but even inside other organisms. Many kinds of marine protozoans can be readily collected from sediments rich in organic debris, the surface of seaweeds, the guts of animals, and plankton samples.

Foraminiferans

Foraminiferans (phylum **Granuloreticulosa**), often called **forams,** are marine protozoans that usually have a shell, or **test,** made of **calcium carbonate ($CaCO_3$).** The test is usually microscopic and may have several chambers (Fig. 5.11*a*), which increase in size as the foram grows. Foraminiferans have long, thin, retractable **pseudopodia**—extensions of the **cytoplasm.** The pseudopodia protrude through pores in the shell and form a network used to trap diatoms and other organisms suspended in the water (see Fig. 15.5). Food is then moved into the interior of the cell as if on a conveyor belt.

Most foraminiferans live on the bottom, either free or attached. Attached forams may develop into conspicuous growths as much as 5 cm (2 in.) in diameter (Fig. 5.11*b*). Each growth consists of a single cell that forms a shell, though some may be covered with

Biogenous Sediments Sediments made of the skeletons and shells of marine organisms; *siliceous ooze* is made of silica, *calcareous ooze* of calcium carbonate.

- Chapter 2, p. 32

Cellulose A complex carbohydrate characteristic of plants and other primary producers.

- Chapter 4, p. 65

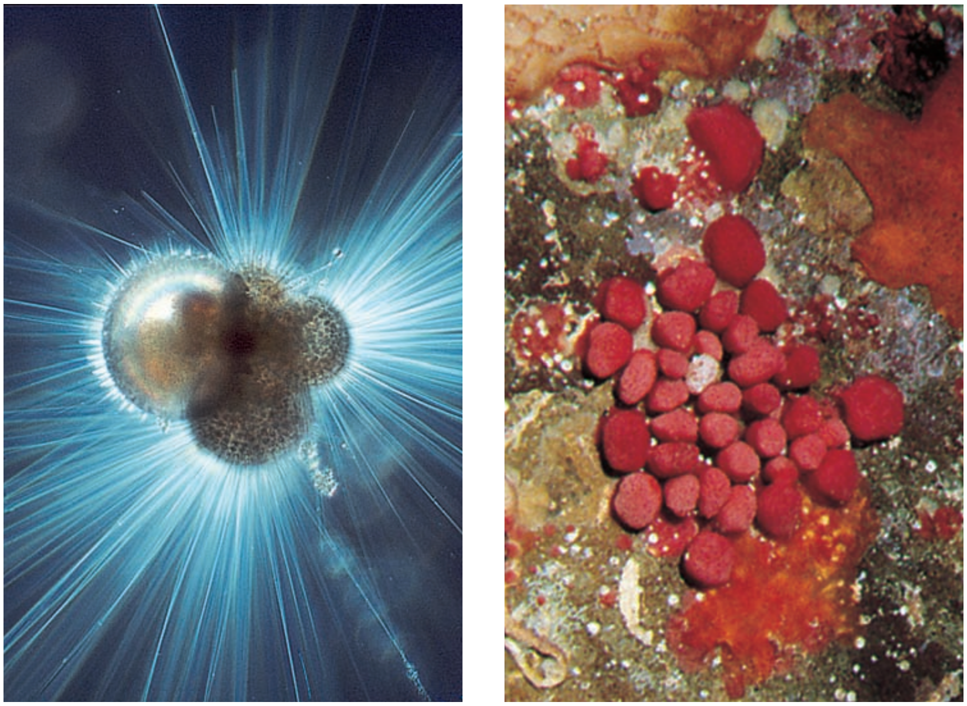

(a) (b)

FIGURE 5.11 Foraminiferans. (*a*) Foraminiferans typically have calcareous shells that consist of a spiral arrangement of chambers. The thin, long strands are the pseudopodia used to capture food. (*b*) *Homotrema rubrum* is a foraminiferan that forms bright red calcareous growths several millimeters in diameter at the base of corals in the tropics. It is so common in Bermuda that its skeletons are responsible for the island's famous pink beaches.

sand grains or other materials instead. The shells of bottom-living foraminiferans can be important contributors of calcareous material on coral reefs and sandy beaches. Relatively few species are planktonic, but these can be very abundant. Their shells are smaller and thinner than those that live on the bottom and may have delicate spines that aid in flotation. The shells of planktonic foraminiferans eventually sink to the bottom in such high numbers that large stretches of the ocean floor are covered by **foraminiferan ooze,** a type of calcareous ooze. Many limestone and chalk beds around the world, such as the white cliffs of Dover in England, are products of foraminiferan sediments that were uplifted from the ocean floor.

Foraminiferans (forams) are protozoans characterized by a shell usually made of calcium carbonate. Most live on the bottom. The shells of planktonic species are important components of marine sediments.

Most species of forams are known only as microfossils (see Fig. 2.17). The distribution of these microfossils in sediments is important to geologists. Shells of warm-water species are slightly larger and more porous than those from colder water. Past water temperatures can be estimated from the distribution of certain marker species. Their distribution is a good indicator of the right type of environment for the formation of oil, as well as the age of sediments.

Radiolarians

Radiolarians (phylum **Polycystina**) are planktonic marine protozoans that secrete elaborate and delicate shells made of glass (silica) and other materials. Typical shells are spherical with radiating spines (Fig. 5.12), though the structure varies (see photo on p. 85). Thin, needle-like pseudopodia capture food, as in foraminiferans.

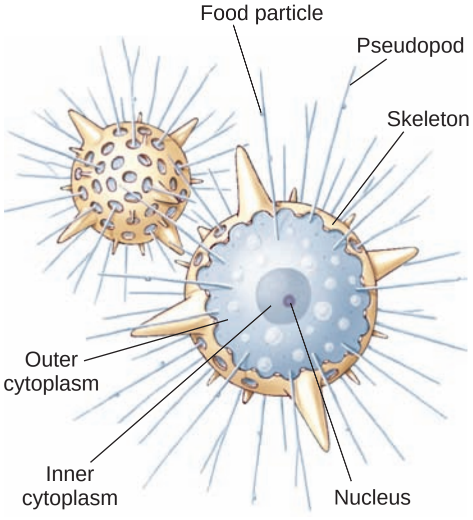
Most radiolarians are microscopic, but some form sausage-shaped colonies that reach 3 m (9 ft) in length, making them true giants among protozoans. Radiolarians inhabit open water throughout the oceans. When abundant, the remains of their shells settle to the bottom and form a siliceous ooze known as **radiolarian ooze.** This ooze is more extensive in deep water because radiolarian shells are more resistant to dissolving under pressure than those of forams.

The shells of radiolarians are made primarily of silica (glass). These shells form siliceous sediments that cover large areas of the ocean floor.

Ciliates

Ciliates (phylum **Ciliophora**) are protozoans that have many hair-like **cilia,** which are used in locomotion and feeding. The most familiar ciliates are freshwater forms, such as *Paramecium.* Many marine ciliates are found creeping over seaweeds and in

FIGURE 5.12 A typical radiolarian cell consists of a dense central portion surrounded by a less dense zone that is involved in the capture of food particles and in buoyancy.



bottom sediments. Some live on the gills of clams, in the intestines of sea urchins, on the skin of fishes, and in other unusual places. Other ciliates live attached to surfaces, even forming branched colonies of tiny individuals. **Tintinnids** are common ciliates that drift in the water and build vase-like cases, or **loricas,** loosely fitting shells that drift in the water (Fig. 5.13). The cases may be transparent or made of bits of particles. Planktonic ciliates are important in the so-called microbial loop of open-water food webs, which facilitates the flow of energy from dissolved organic matter to the larger plankton (see Fig. 15.25).

FUNGI

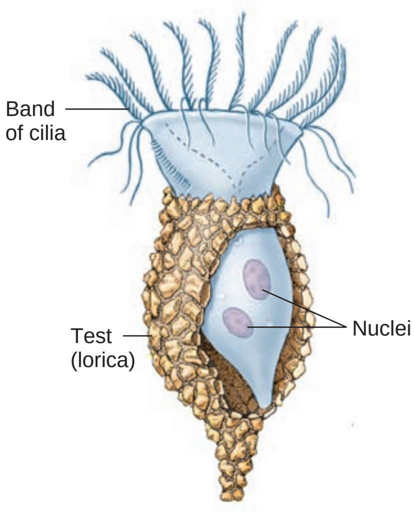
Fungi (kingdom **Fungi**) are eukaryotic and mostly multicellular, though some, such as molds and yeasts, are unicellular. Fungi are heterotrophs that lack chloroplasts and chlorophyll and cannot perform photosynthesis.

There are at least 1,500 known species of marine fungi. They are mostly microscopic. Many, as in bacteria, decompose detritus. They are the most important decomposers of dropped mangrove leaves and thus contribute to the recycling of nutrients in mangrove forests (see "Mangrove Forests," p. 276). Some are parasites of seagrasses or borers in mollusc shells. Others are parasites that cause diseases of economically important seaweeds, sponges, shellfish, and fishes. Some marine fungi are being investigated as a source of antibiotics for use in medicine.

Some fungi live in symbiotic associations mostly with green algae or cyanobacteria to form unique entities, the **lichens.** In lichens the long, filament-like growths of the fungi provide support, whereas the algae or cyanobacteria provide food from photosynthesis. Marine lichens can be typically found as thick, dark brown or black patches in the wave-splashed zone of exposed rocky shores (Fig. 5.14). They are tolerant to exposure to air for long periods of time.

By comparison with the multitude of lichens on land, there are very few types of marine lichens. Their role on the ecology of rocky shores is largely unknown. The cyanobacteria of some marine lichens are known to be nitrogen-fixers. Some lichens are able to loosen bits of the rocks where they live by growing into the rock. A few types live on the shells of rocky shore barnacles and limpets.

FIGURE 5.13 *Tintinnopsis* is a marine tintinnid that forms a vase-like lorica made of sand grains. Specialized cilia on one end are used in feeding.



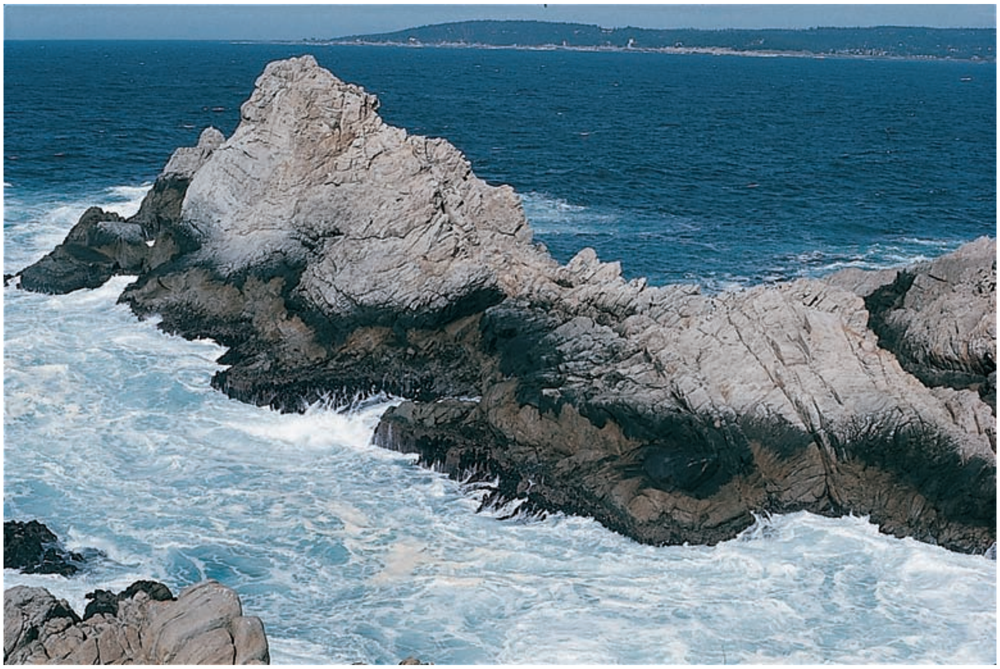
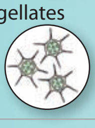
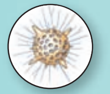


FIGURE 5.14 Encrusting marine lichens, cyanobacteria, and some microscopic algae are often visible as a dark band on wave-splashed rocky shores, as in this exposed rocky point south of Monterey Bay, California.

Table 5.2 Most Important Characteristics of Marine Microbes

Group	Distinguishing Features	Photosynthetic Pigments	Major Food Reserves	Major Cell-Wall or Cell-Membrane Components	Significance in the Marine Environment
Viruses	Non-cellular; parasites of all organisms	None	None	Capsid of protein, sometimes lipids	Infect all marine organisms; release dissolved organic matter (DOM) from destroyed cells
Bacteria	Prokaryotic, unicellular; some form colonies	Chlorophyll *a*, phycobilins, carotenoids in cyanobacteria; bacteriochlorophyll in other photosynthetic bacteria	Variety of types	Cell wall of peptidoglycan containing muramic acid; chains of amino sugars and amino acids in cyanobacteria	Essential role in nutrient cycles; autotrophs (especially cyanobacteria) and heterotrophs, including decomposers; nitrogen fixers; components of detritus; some cause diseases; symbiotic in many organisms; some produce blooms
Archaea	Prokaryotic, unicellular;	Bacteriorhodopsin in light-capturing archaea	Variety of types	Cell wall made up of variety of compounds but no muramic acid	Autotrophs and heterotrophs; nitrogen fixers
Diatoms	Eukaryotic, unicellular; some form chains; mostly planktonic	Chlorophyll *a*, *c*, carotinoids	Chryso-laminarin, oil	Cell membrane secretes frustule of silica, pectin	Important primary producers; frustules are components of siliceous sediments
Dinoflagellates	Eukaryotic, unicellular; two flagella; mostly planktonic, some bottom-dwelling	Chlorophyll *a*, *c*, carotenoids	Starch, oil	Cell membrane secrets cellulose plates (thecae)	Primary producers; symbiotic with other organisms as zooxanthellae; red tides; many are bioluminescent; some cause diseases *(Pfiesteria)*
Silicoflagellates 	Eukaryotic, unicellular; two flagella; planktonic	Chlorophyll *a*, *c*, fucoxanthin	Starch	Cell membrane secretes silica skeleton	Primary producers; skeletons are component of siliceous sediments; some produce blooms
Coccolithophorids	Eukaryotic, unicellular; 1-2 flagella; planktonic	Chlorophyll *a*, *c*, carotenoids	Starch	Cell membrane secretes calcium carbonate plates	Important primary producers; plates are components of calcareous sediments; some produce blooms
Cryptophytes	Eukaryotic, unicellular; usually 2 flagella; planktonic	Chlorophyll *a*, *c*, carotenoids, phycopilins	Variety of types	Cell membrane made up mostly of protein	Important primary producers
Foraminiferans	Eukaryotic, unicellular; bottom-dwelling and planktonic	None	Variety of types	Cell membrane secretes calcium carbonate shell (test)	Heterotrophs; shells are components of calcareous sediments
Radiolarians 	Eukaryotic, unicellular; some colonial; mostly planktonic	None	Variety of types	Cell membrane secretes silica shell	Heterotrophs; shells are components of siliceous sediments
Ciliates	Eukaryotic, unicellular; planktonic and bottom-dwelling	None	Variety of types	Cell membrane made up mostly of lipids	Heterotrophs; some associated with marine animals
Fungi	Eukaryotic, unicellular, multicellular; mostly bottom-dwelling	None	Variety of types	Cell wall of cellulose, chitin, and other compounds	Decomposers, many cause diseases; symbiotic with algae or cyanobacteria in lichens

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Scientists use the particular structure of nucleic acids and other chemical differences to separate the archaea from the bacteria. Can you think of other characteristics that could be used to distinguish not only between these two domains but also between them and protists?
2. An autotrophic protist, such as a diatom or a dinoflagellate, can evolve into a heterotrophic protist (and therefore a protozoan) simply by losing its chloroplasts. Under what conditions might this take place?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Baskin, Y., 2006. Sea sickness: The upsurge in marine diseases. *BioScience,* vol. 56, no. 6, June, pp. 464–469. Demoic acid produced by diatoms and reef coral diseases are among problems that have been recently investigated.

Cohen, P., 2004. Natural glass. *New Scientist,* vol. 181, no. 2430, 17–23 January, pp. 26–29. Diatoms could have useful applications in nanotechnology by serving as inexpensive, easy-to-obtain microscopic devices.

Gast, R., 2004. Revealing the ocean's invisible abundance. *Oceanus,* vol. 43, no. 2, pp. 64–67. New instruments are used to study marine microbes.

Hamilton, G., 2005. Mother superior. *New Scientist,* vol. 187, no. 2515, Sept. 3–9, pp. 26–29. Several hypotheses aim at explaining the nature of the early prokaryotes ancestral to all living things.

Kasting, J. F., 2004. When methane made climate. *Scientific American,* vol. 291, no. 1, July, pp. 78–85. Methanogens, a large group of archaea, were responsible for the methane-rich, oxygen-poor atmosphere of the early earth. It all changed with the appearance of photosynthetic cyanobacteria, which gradually replaced methane with oxygen.

Lee, R. F. and M. E. Frischer, 2004. The decline of the blue crab. *American Scientist,* vol. 92, no. 6, November/December, pp. 548–533. A parasitic dinoflagellate that develops in the tissues of the blue crab has caused a decline in the number of blue crabs on the east coast of the United States.

Niklas, K. J., 2004. The cell walls that bind the Tree of Life. *BioScience,* vol. 54, no. 9, pp. 831–841. Symbiosis appears to have played an important role in the evolution of cell walls in prokaryotes as well as in eukaryotes.

Malin, M. A., 2006. Wading in waste. *Scientific American,* vol. 294, no. 6, June, pp. 52–59. Disease-causing microbes pollute beaches and seafood as a result of unchecked development.

Russel, M., 2006. First life. *American Scientist,* vol. 94, no. 4, January/February, pp. 32–39. The prokaryotes that first appeared on earth evolved in unique environments.

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Silver, M. W., 2006. Protecting ourselves from shellfish poisoning. *American Scientist,* vol. 94, no. 4, July/August, pp. 316–325. Molecular probes and other new techniques are used to monitor the appearance of harmful algae that cause shellfish poisoning, ciguatera, and other deadly diseases.

Teske, A. and K. Edwards, 2004. The deeps of time in the depth of the ocean. *Oceanus,* vol. 43, no. 2, pp. 17–19. Recently discovered groups of microbes have changed our views on the evolution of life.

Waterbury, J., 2004. Little things matter a lot. *Oceanus,* vol. 43, no. 2, pp. 12–16. Cyanobacteria are one of the most important groups of organisms on earth.

In Depth

Canfield, D. E., E. Kristensen, and B. Thamdrup, 2005. Aquatic geomicrobiology. *Advances in Marine Biology,* vol. 48, pp. 1–636.

Fernández, L. A., 2005. Exploring prokaryotic diversity: There are other molecular worlds. *Molecular Microbiology,* vol. 55, no. 1, pp. 5–15.

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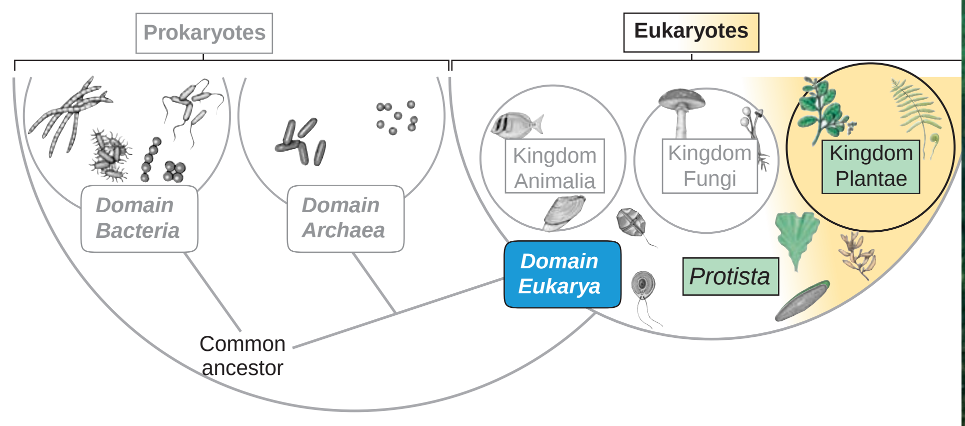
Multicellular Primary Producers: Seaweeds and Plants



Rocky-shore seaweeds, Bay of Biscay, Spain.

As inhabitants of land, our perception of the world of photosynthetic organisms is based mostly on plants such as trees, ferns, and mosses. Many fascinating photosynthetic organisms populate the oceans, but for the most part they are very different from the land plants that surround us. Most, in fact, are not considered plants at all and therefore are not members of the kingdom Plantae. Non-plant photosynthetic organisms include photosynthetic bacteria and unicellular algae (both described in Chapter 5) and the seaweeds covered here. Some biologists, however, consider some or all seaweeds to be plants.

What makes practically all the organisms covered in this chapter "plant-like" is that they are **primary producers** capable of using light energy to perform photosynthesis, like photosynthetic bacteria and the unicellular algae. There are always exceptions, and there are a few seaweeds that are not primary producers but parasites of other seaweeds.

Seaweeds play an important role in many coastal environments. Seaweeds transform solar energy into chemical energy in the form of organic matter and make it available to a long list of hungry creatures, which may include humans. Other organisms live on or even in the tissues of seaweeds. Seaweeds also produce oxygen for organisms both on land and in the ocean.

MULTICELLULAR ALGAE: THE SEAWEEDS

The most familiar types of marine algae are those popularly known as **seaweeds,** which is a rather unfortunate term. For one thing, the word "weeds" does not do justice to these conspicuous and often elegant inhabitants of rocky shores and other marine environments. Some biologists opt for the more formal name of **macrophytes** or **macroalgae.** On the other hand, the term "seaweeds" is useful in distinguishing them from the unicellular algae surveyed in Chapter 5 and the seagrasses and salt-marsh grasses described later in this chapter. By definition, seaweeds are all multicellular; unicellular green and red algae are therefore not considered seaweeds. The classification of seaweeds takes into consideration not only structure but also other features, such as the types of pigments and food products they store (see Table 6.1 p. 113).

Like unicellular algae, seaweeds are eukaryotic. The structures of seaweeds, however, are far more complex than those of unicellular algae. Reproduction is also more elaborate. Though more complex than unicellular algae, seaweeds nevertheless lack the highly specialized structures and reproductive mechanisms of the mostly terrestrial plants.

The range of variation observed among seaweeds is spectacular. Those we see on rocky shores at low tide are usually small and sturdy as an adaptation to withstand waves. Some small, delicate ones live on other seaweeds. Kelps found offshore in cold waters are true giants that form dense underwater forests (see Fig. 6.8*b*).

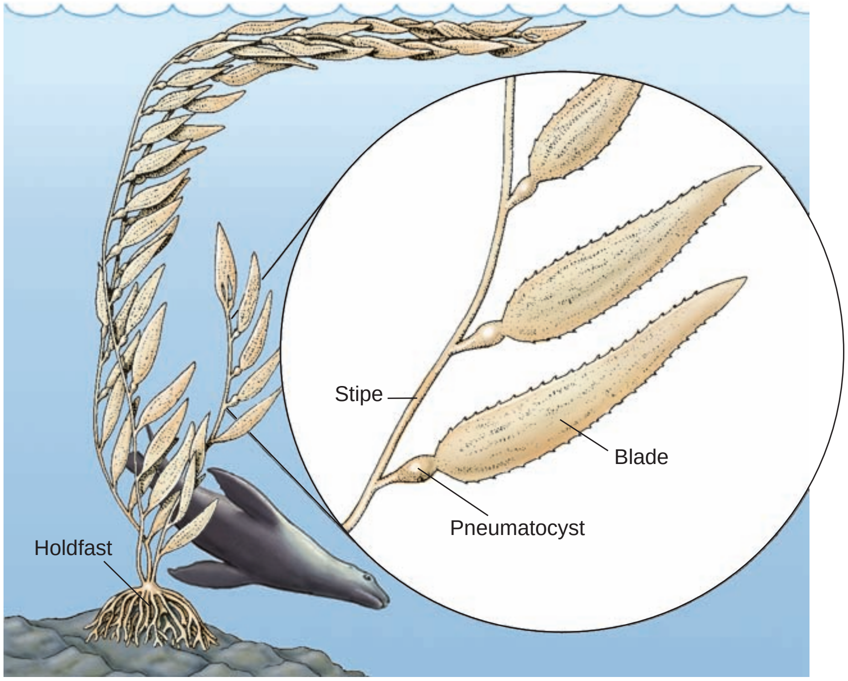


FIGURE 6.1 The giant kelp (*Macrocystis*).

The multicellular condition of seaweeds allows many adaptations not available to unicellular forms. The ability of seaweeds to grow tall and rise off the bottom provides new opportunities as well as challenges, particularly that of wave action.

General Structure

Seaweeds show a wide range of growth forms and complexity of structures. Nevertheless, several unifying features are worth mentioning. Seaweeds lack the true leaves, stems, and roots of plants. The complete body is known as the **thallus** (plural, **thalli**) whether it is a filament, a thin leafy sheet, or a giant kelp.

The leaf-like, flattened portions of the thallus of many seaweeds are known as **blades** (Fig. 6.1). They have a large surface area and are the main photosynthetic regions, though all portions of the thallus are able to photosynthesize in light as long as they have chlorophyll. Blades are technically not true leaves because they have no veins. Another difference is that, in contrast to true leaves, the upper and lower surfaces of blades are identical to each other. Gas-filled bladders known as **pneumatocysts** (Fig. 6.1) sometimes keep the blades close to the sea surface, thereby maximizing their exposure to the sunlight. The mixture of gases in the pneumatocysts of some seaweeds includes carbon monoxide, a gas that is toxic to humans.

Some seaweeds have a distinct, stem-like structure to provide support, the **stipe,** from which blades originate. It is long and tough in the large kelps. A structure that looks like roots, the **holdfast,** attaches the thallus to the bottom. Holdfasts are particularly well developed in the kelps (Fig. 6.1). They are not involved in any significant absorption of water and nutrients and do not penetrate through the sand or mud, as true roots do. Most seaweeds cannot anchor in soft sediments and are therefore restricted to hard bottoms. Water and nutrients, which bathe the entire thallus, are picked up directly across the surface without the need of roots. Also, in contrast to the leaves and stems of plants, the stipe and holdfast usually lack tissues specialized for water and nutrient transport.

Seaweeds typically consist of a thallus, which is sometimes provided with leaf-like blades, and a root-like holdfast. They lack true leaves, stems, or roots.

Types of Seaweeds

There are three types of seaweeds: the green, brown, and red algae. It is not always easy to recognize the groups by their color in nature because the proportion of chlorophyll and other pigments (see Table 6.1) can vary. Chemical analysis, however, reveals the characteristic pigments of each group.

Green Algae Most **green algae** (division, or phylum, **Chlorophyta**) live in freshwater and terrestrial environments. Only around 10% of the estimated 7,000 species are marine; many of these marine species are unicellular. This, however, does not mean that multicellular green algae are uncommon in the sea. Certain species dominate in environments with wide variations in salinity, such as bays and estuaries and isolated tide pools on rocky coasts.

Primary Producers Organisms that manufacture organic matter from CO_2, usually by photosynthesis.
- Chapter 4, p. 68

Most multicellular green algae have a simple thallus compared to the other two groups of seaweeds. Their pigments and food reserve are the same as those in plants (see Table 6.1, p. 113), so it is thought that land plants evolved from green algae. Chlorophyll in both green algae and plants is not normally masked by any other pigments, and green algae typically have a bright green thallus.

Multicellular green algae are common in some marine environments. They are typically bright green because chlorophyll is not masked by other pigments.

Filamentous green algae may be common on rocks in shallow water and other seaweeds, as well as in rocky shore tide pools. The filaments of these species may be branched or unbranched. Species of *Enteromorpha* have a thin thallus in the form of a hollow tube. They sometimes flourish in polluted areas. Sea lettuce (*Ulva;* Fig. 6.2) forms paper-thin sheets whose shape varies depending on environmental factors. Different species of *Ulva* are widespread, from polar to tropical waters. *Valonia* forms large spheres or clusters of spheres in the tropics and subtropics.

Several other green algae consist of thin filaments or tubes (siphons) formed by a single giant cell with many nuclei. Such is the case in *Caulerpa*, which is restricted to the tropics and subtropics. Its many species show a great variety of shapes. Dead man's fingers (*Codium;* Fig. 6.3) is a green alga that extends from tropical to temperate waters, including both coasts of North America. It consists of multinucleated filaments woven into a spongy, often branching thallus. The thallus of *Halimeda*, a **calcareous green alga,** consists of numerous segments with deposits of calcium carbonate (see Fig. 14.10). The accumulation of its dead, calcified segments plays an important role in the formation of coral reefs (see "Other Reef Builders," p. 307; "Coral Reef Seaweeds," p. 105).

FIGURE 6.2
Ulva, or sea lettuce, is a green alga that is common on rocks where fresh water, often containing high amounts of nutrients, reaches the sea.

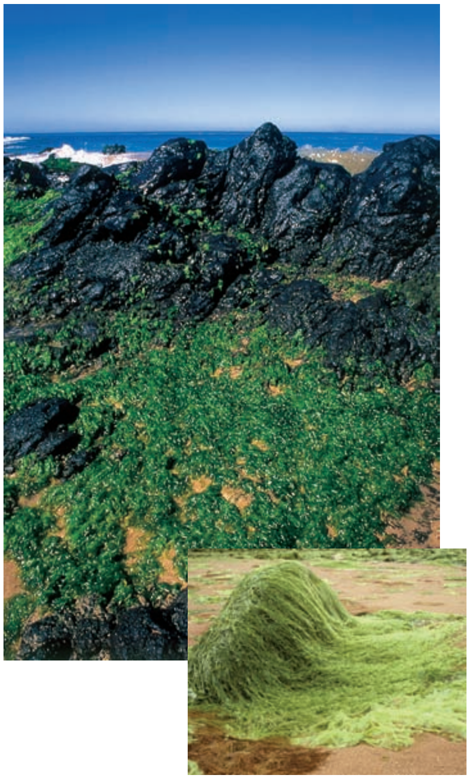
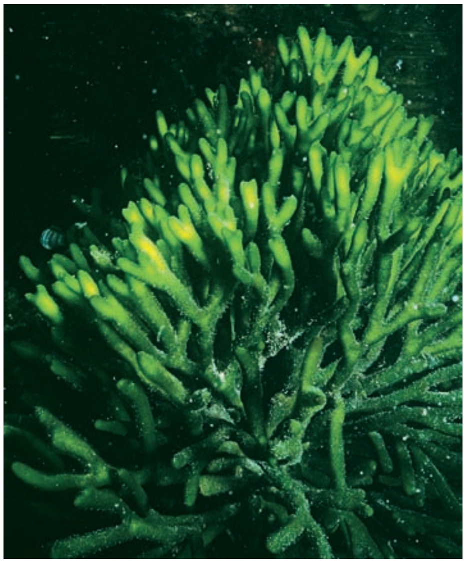


FIGURE 6.3
The dead man's fingers (*Codium fragile*) form branched clumps on rocky shores. Its chloroplasts remain alive, and still photosynthesize, in sea slugs (shell-less gastropods) that feed on the seaweed.



Brown Algae The color of the **brown algae** (division, or phylum, **Phaeophyta**), which actually varies from olive green to dark brown, is due to a preponderance of yellow-brown pigments, particularly **fucoxanthin,** over chlorophyll. (See Table 6.1, p. 113). Almost all the approximately 1,500 known species are marine. Brown algae are often the dominant primary producers on temperate and polar rocky coasts and include the largest and most complex seaweeds.

The brown algae have yellow-brown pigments in addition to chlorophyll. They include the largest and structurally most complex seaweeds.

The simplest brown algae have a finely filamentous thallus, as in the widely distributed *Ectocarpus.* The thallus is flat and branched in *Dictyota* and fan-shaped and lightly calcified in *Padina* (Fig. 6.4). Both are tropical and subtropical. The thallus of most species of *Desmarestia* is branched in many ways. *Desmarestia* is found in cold waters. It ranges from the Antarctic, where it is one of the dominant species, to temperate shores elsewhere.

Some of the most conspicuous of all brown algae are those exposed at low tides at the middle and upper levels of rocky shores. Their thick, leathery thalli can withstand exposure to air (see "Exposure at Low Tide," p. 242). Many species have gas-filled floats. Known locally as **rockweeds,** or **wracks,** *Fucus* (Fig. 6.5) is found on the Atlantic and Pacific coasts of North America and other temperate shores. The knotted seaweed (*Ascophyllum;* Fig. 6.6) is found along temperate Atlantic coasts. In warm waters, including the Gulfs of Mexico and

EYE ON SCIENCE

Coral Reef Seaweeds

Seaweeds are not often regarded as important components of healthy coral reefs, mostly because reefs impacted by pollution and other detrimental factors very often become overrun by seaweeds (see Fig. 14.14). Recent research by the Coral Reef Ecosystem Division (CRED) of the United States' Ocean and Atmospheric Administration (NOAA) has shown, however, that some highly diverse, healthy coral reefs in pristine environments from the relatively isolated central Pacific Ocean are dominated by seaweeds rather than by corals or other types of marine organisms. Such a surprising finding has challenged marine biologists to revise their views on the role of seaweeds in coral reefs, while still recognizing that reefs are built by colonial reef animals, their symbiotic zooxanthellae, and coralline algae (see "The Organisms That Build Reefs," p. 303).

Hundreds of species of coral reef algae are known, each with their own unique morphological and functional attributes. This vast algal diversity is typically reduced by reef biologists into three major functional groups. Turf algae consist of a group of small, filamentous seaweeds that cover essentially all non-living hard surfaces on the reef, including dead coral and spaces between live coral colonies. They are the first to colonize any vacant surfaces on the reef. Coralline algae, the second group, are red algae that produce a hard calcareous skeleton (see "Red Algae," p. 106). Some reef biologists believe that coralline algae literally hold coral reefs together. The third group belongs to macroalgae, typically fleshy seaweeds that are larger in size and therefore more obvious to the observer than those in the first two groups. *Halimeda* (see Fig. 14.10) is a calcareous green macroalga that together with the coralline algae plays an important role in the deposition of calcium carbonate in coral reefs.

Understanding the role of algae in healthy coral reefs is what stimulated some of the recent research conducted by NOAA in the central Pacific. The distribution of algae on reefs was studied using techniques such as video-transects, photoquadrats, and towed-diver surveys. Hundreds of species of tropical macroalgae are common components of coral reef ecosystems, yet they remain among the least-understood and least-studied of all coral reef inhabitants. Their abundance can vary, increasing with rising water nutrients, which are typically very low in tropical regions. Grazers, like sea urchins, molluscs, and fishes, keep their numbers down.

Results of field work in central Pacific coral reefs, particularly in the subtropical Northwestern Hawaiian Islands, showed that fleshy macroalgae were dominant in many of the healthy reefs of the region, often forming expansive meadows spanning acres and serving as critical habitats for numerous invertebrates and juvenile fishes. Macroalgae occupied as much as or even more surface area than live reef corals in 46% of the sites that were studied. Some of the macroalgae even proved to be species new to science. Coralline algae, once thought to be slow growing, are now known to grow fast, and probably playing previously unknown roles. The algae have been found, for instance, to produce substances that stimulate the settlement of the larvae of corals and other invertebrate animals. Ongoing research by the NOAA team is also geared towards understanding the effect of grazers, nutrients, and other factors on the species diversity and relative abundance of macroalgae over time, and, most of all, seeking answers to one critical question: Are these changes good environmental indicators of the reef health?

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

California, these temperate species are replaced by sargasso weed (*Sargassum*). Sargasso weed has spherical air bladders that keep the small, leaf-like blades afloat at the sea surface. Most species grow on rocks, but at least two float offshore in huge masses. The **Sargasso Sea,** an area in the Atlantic north of the West Indies (see Fig. 8.24), takes its name from sargasso weed. The seaweed drifts in other regions of the world as well. It is particularly common in the Gulf of Mexico.

The **kelps** are the most complex and largest of all brown algae. Most kelps are found below the low tide level in temperate and subpolar latitudes. In these environments they can occur in great abundance, providing food and shelter for many other organisms.

Some kelps consist of a single large blade, up to 3 m (almost 10 ft) in length, as in the many species of *Laminaria* (see Figs. 13.21 and 13.26). Their blades are harvested for food in several parts of the world (see "Seaweeds for Gourmets," p. 111). Several blades may grow from a single holdfast. In some species of *Laminaria* the blade is split or branched. In

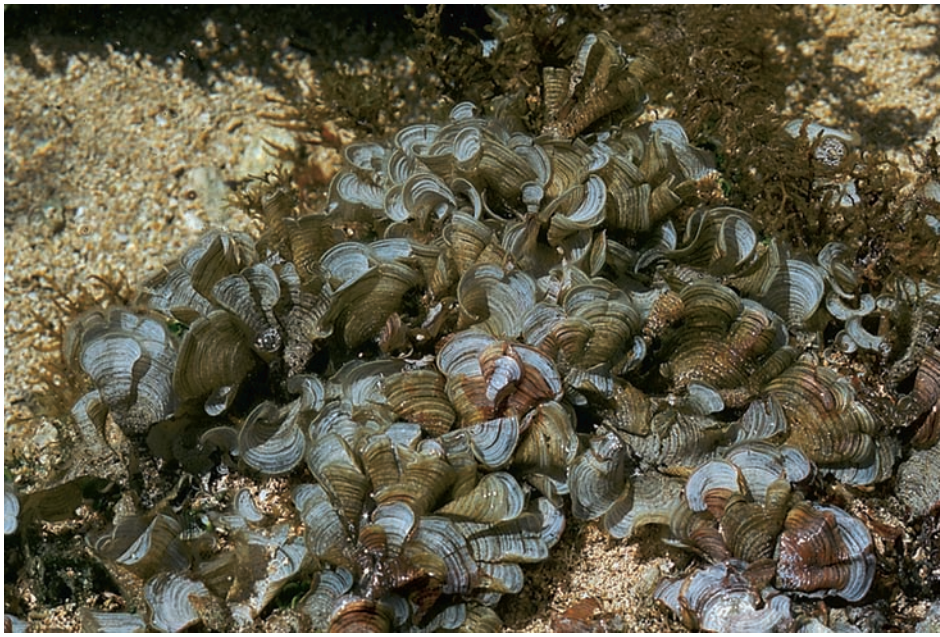


FIGURE 6.4 *Padina,* a brown alga, consists of clusters of flat blades that are rolled into circles. This species is from the Hawaiian Islands.

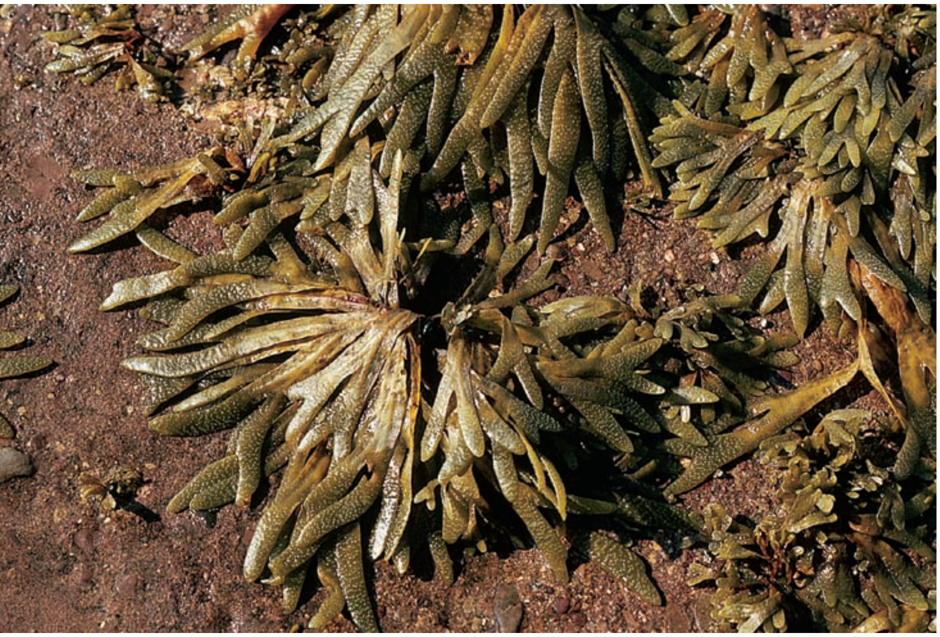


FIGURE 6.5 The spiral rockweed (*Fucus spiralis*) is common on rocky shores on the Atlantic coasts of temperate North America and Europe. Its thallus lacks the air bladders that characterize a similar species, the bladder rockweed (*Fucus vesiculosus*).

Agarum and *Alaria* (see Fig. 13.21), a conspicuous rib runs along the middle of the single blade. The blade of *Alaria* can be as long as 25 m (82 ft). *Postelsia,* commonly known as the sea palm because of its appearance (Fig. 6.7), grows on intertidal rocks exposed to heavy waves. It occurs in thick clusters from central California to British Columbia. Two branched forms, the feather-boa kelp (*Egregia;* see Fig. 13.26) and the southern sea palm (*Eisenia*), are also common on Pacific rocky shores.

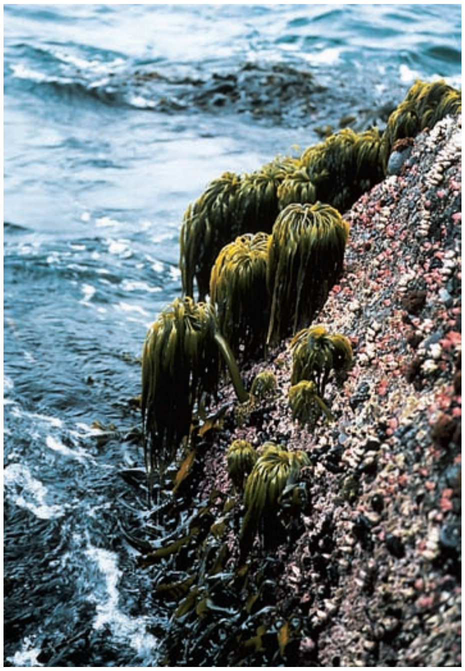
In the Pacific the largest kelps are found in deeper water just below the lowest tide level. The bull kelp, *Nereocystis*, consists of a whip-like stipe up to 30 m (almost 100 ft) long with a large, spherical pneumatocyst at the upper end (see Fig. 13.26). Another large kelp is *Pelagophycus* (see Figs. 13.23 and 13.26). It is similar to the bull kelp, but it has impressive antler-like branches.

FIGURE 6.6 The knotted rockweed (*Ascophyllum nodosum*) occurs on the North American and European coasts of the North Atlantic.

Macrocystis (see Fig. 6.1) is the largest of the kelps. Its massive holdfast is attached to hard bottoms. Several long stipes grow from the holdfast, from which elongated blades develop (Fig. 6.8*a*). At the base of each blade a gas-filled pneumatocyst eventually develops, which helps keep the blades close to the surface. Individuals as long as 100 m (330 ft) have been recorded. It has been estimated that such kelps can grow 50 cm (20 in.) or more per day in optimal conditions. Many individuals, each with many fast-growing and intertwined stipes, form dense and very productive **kelp beds,** or **forests** (Fig. 6.8*b*), in the colder waters of the North and South Pacific (see the map in Fig. 13.22). Kelp beds are harvested by chopping off the tops for the extraction of several natural products (see “Economic Importance,” p. 109). Kelp beds are among the richest, most productive environments in the marine realm and will be discussed under “Kelp Communities” (p. 296).

Red Algae There are more species of marine **red algae** (division, or phylum, **Rhodophyta**) than of marine green and brown algae combined. Among other features, they have red pigments called **phycobilins,** which mask chlorophyll (see Table 6.1, p. 113). Most species actually are red, though some may have different colors depending on their daily exposure to light. The group is essentially marine; only a few of the approximately 4,000 species live in fresh water or soil. Red algae inhabit most shallow-water marine environments. Some are harvested for food and for the extraction of various products (see “Economic Importance,” p. 109).

FIGURE 6.7 Stands of the sea palm (*Postelsia palmaeformis*) are common on rocky shores exposed to heavy wave action on the Pacific coast of North America (also see Figs. 11.13 and 11.17).



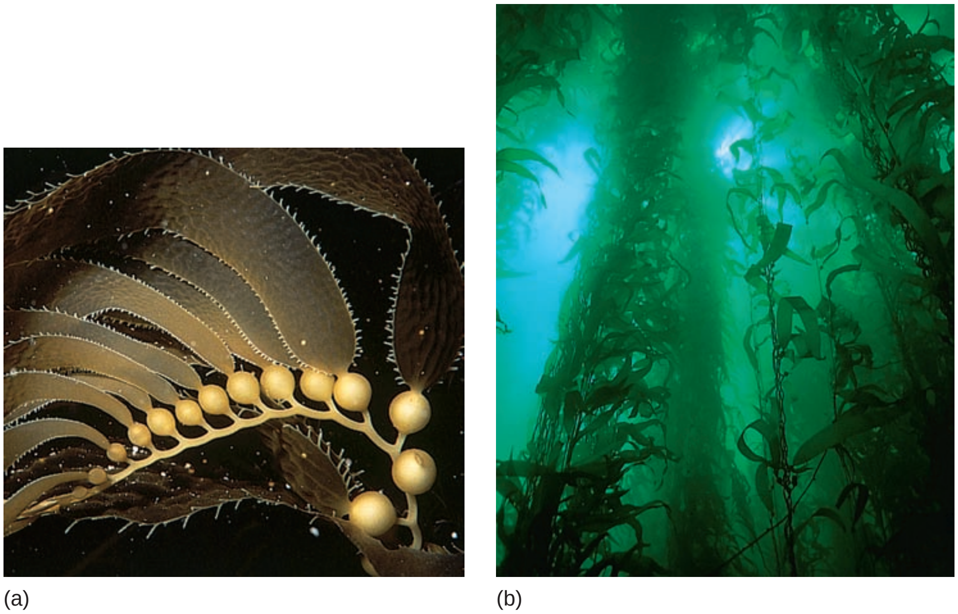
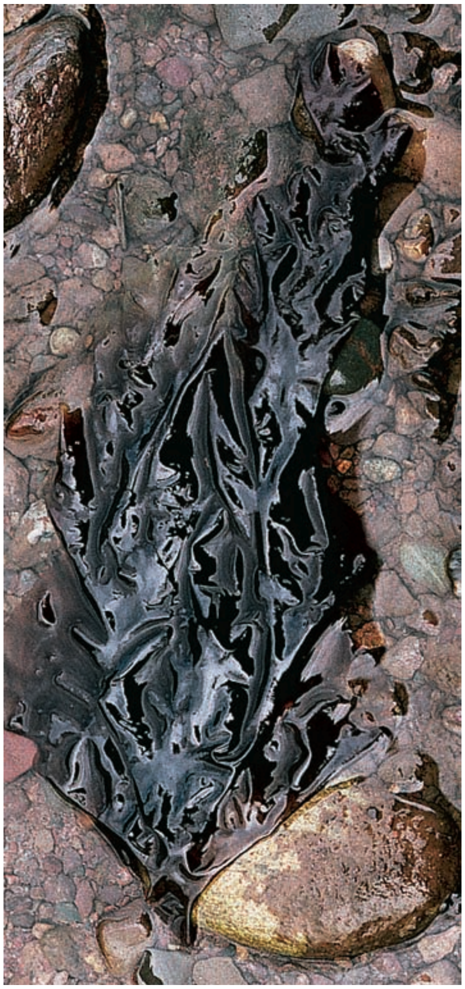

(a)
(b)

FIGURE 6.8 (*a*) The growing end of a stipe of the giant kelp (*Macrocystis pyrifera*). (*b*) A kelp forest in California (also see Figs. 13.24 and 13.26).

The red algae are the largest group of seaweeds. Their chlorophyll is typically masked by a red pigment.

The structure of the thallus of red algae does not show the wide variation in complexity and size seen in brown algae. Some reds have become greatly simplified, at least in their structure, by becoming parasites of other seaweeds. A few have lost all trace of chlorophyll and have become heterotrophs, depending entirely on their host for nutrition. Most red algae are filamentous, but the thickness, width, and arrangement of the filaments vary a great deal. Dense clumps are more common on the upper levels of rocky shores that are exposed at low tide; longer and flatter branches predominate in areas less exposed to air and in deeper water. These variations are observed among the many species of *Gelidium* and *Gracilaria* that are found worldwide. *Endocladia* forms wiry clumps on rocky shores from Alaska to Southern California.

FIGURE 6.9 Many species of *Porphyra,* a red alga, inhabit temperate, polar, and tropical rocky shores around the world. Some are of economic importance.



Some species of *Gigartina* have large blades as long as 2 m (6 ft). These are among the most massive of the red algae. Numerous species of *Porphyra* are common on rocky shores above the lowest tide marks from polar to tropical coasts (Fig. 6.9). The most common growth form is a thallus with thin, large blades. *Rhodymenia* is common in the North Atlantic. Its blades may reach 1 m (3 ft) in length. Irish moss (*Chondrus*) is another North Atlantic red alga. It can tolerate wide ranges of temperature, salinity, and light, and its shape varies greatly in response to these physical factors.

The **coralline algae** are red algae that deposit calcium carbonate within their cell walls. They are important in several marine environments. The calcified thallus takes a variety of shapes: thin disks growing over other seaweeds, branches with many joints (*Corallina;* Fig. 6.10), smooth or rough **encrusting** growths on rocks. The color of live coralline algae typically varies from light to intense reddish-pink; dead ones are white. Warm-water coralline algae are actively involved in the formation and development of Coral reefs (see “Other Reef Builders,” p. 307; “Coral Reef Seaweeds,” p. 105). Other species thrive in temperate and polar waters, often attaining a large size.

Life History

Reproduction is a complex affair in seaweeds. **Asexual,** or vegetative, reproduction is common. It may be more important than **sexual** reproduction in most species. Fragments of the thallus can often grow into new individuals, as occurs in the floating masses of *Sargassum* of Sargasso Sea fame. Some

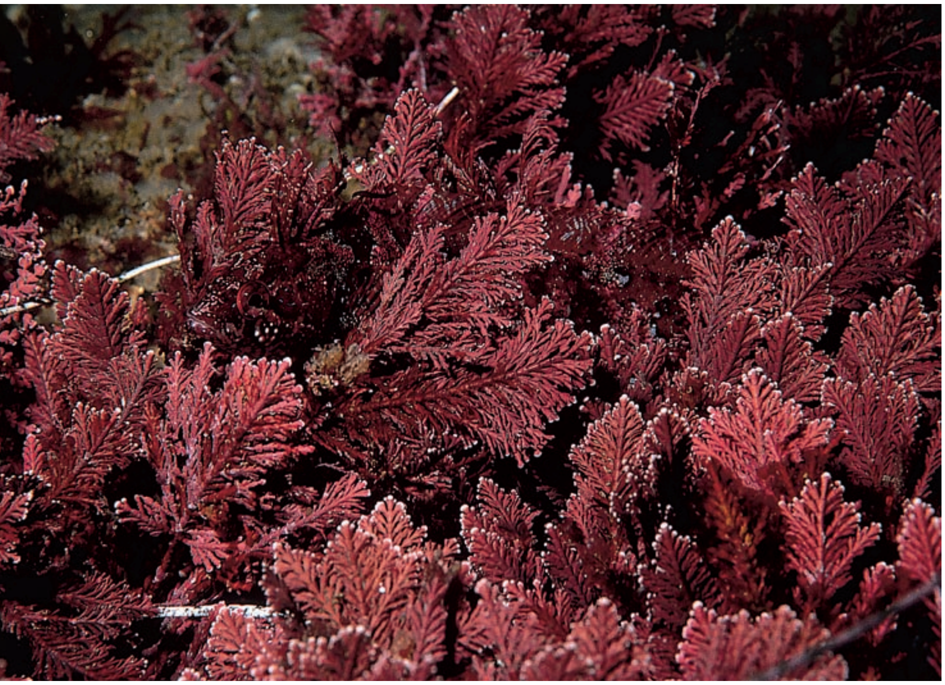


FIGURE 6.10 *Corallina,* a coralline alga.

seaweeds produce **spores,** which are cells specialized for dispersing to new locations or persisting through unfavorable conditions. Some spores are protected by resistant cell walls; others have flagella for movement and are known as **zoospores.**

The production of **gametes** is a key event in sexual reproduction. Gametes from two different individuals fuse, so that the new generation contains genetic information from both parents. Genetic variation is thus ensured generation after generation. Gametes produced by all members of a seaweed species may be similar in appearance or may consist of larger, non-motile eggs and smaller sperm that can swim by means of flagella. Male gametes in the red algae lack flagella and are non-motile. They may be released in strands of slime. Male and female gametes may be formed in the same thallus, but the chances are good that fusing gametes will be from separate thalli.

Cells of seaweeds (and of us all—clam, fish, or human) divide and produce identical cells by **mitosis.** Seaweeds may also produce haploid spores or gametes by **meiosis.** The existence of diploid and haploid cells is fundamental in understanding the often complex life histories of seaweeds. Their life histories can be divided into four basic types.

The first type (Fig. 6.11*a*) is the most common among all three groups of seaweeds, and it involves two types of thalli. The first is a diploid (2*n*) **sporophyte** generation that

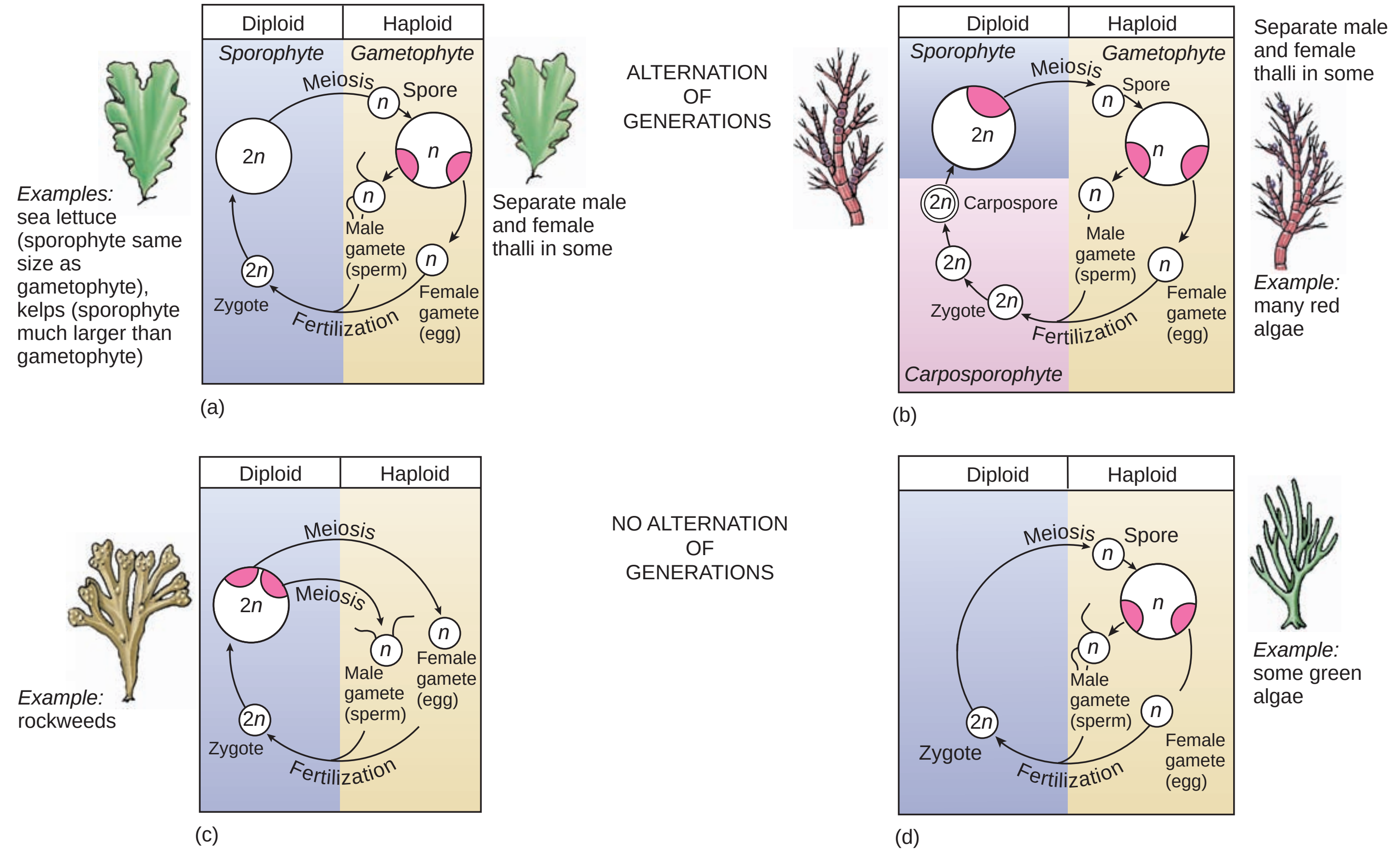

Diploid
Haploid
Sporophyte
Gametophyte
Meiosis
n
Spore
2n
n
n
Male gamete (sperm)
n
Female gamete (egg)
2n
Zygote
Fertilization
Examples:
sea lettuce (sporophyte same size as gametophyte),
kelps (sporophyte much larger than gametophyte)
Separate male and female thalli in some
(a)
ALTERNATION OF GENERATIONS
Diploid
Haploid
Sporophyte
Gametophyte
Meiosis
n
Spore
2n
n
2n
Carpospore
n
Male gamete (sperm)
n
Female gamete (egg)
2n
2n
Zygote
Fertilization
Carposporophyte
Separate male and female thalli in some
Example:
many red algae
(b)
Diploid
Haploid
Meiosis
Meiosis
2n
n
Male gamete (sperm)
n
Female gamete (egg)
2n
Zygote
Fertilization
Example:
rockweeds
(c)
NO ALTERNATION OF GENERATIONS
Diploid
Haploid
Meiosis
n
Spore
n
n
Male gamete (sperm)
n
Female gamete (egg)
2n
Zygote
Fertilization
Example:
some green algae
(d)

FIGURE 6.11 Basic patterns of sexual reproduction in the life histories of seaweeds. These patterns are not absolute, and many modifications have been described. In some groups certain reproductive stages have different names.

through meiosis produces not gametes but haploid (*n,* or 1*n*) spores. Except in the red algae, these spores are typically motile. They divide and develop into the second kind of thallus, a haploid (*n*) **gametophyte** generation. The gametophyte is the one that produces haploid gametes. In some species there are separate male (sperm-producing) and female (egg-producing) thalli; in others, both types of gametes are produced by every thallus. The gametes are released and, on fertilization, produce a diploid (2*n*) zygote that develops into the diploid sporophyte. A life history with two generations, a sporophyte and a gametophyte, is an example of the phenomenon of **alternation of generations**. In some algae, such as sea lettuce (*Ulva*) and the brown *Dictyota,* the sporophyte and gametophyte are structurally identical. On the other hand, in kelps (*Laminaria, Macrocystis* and others) the large plant we see is the sporophyte, whereas the gametophyte is minute and barely visible (see Fig. 13.25). A similar type of alternation of generations takes place in flowering plants, when a sporophyte dominates over a minute gametophyte.

The second type of life history, unique to the red algae, is more complex, involving alternation of three generations (Fig. 6.11*b*). It is similar to the life history illustrated in Figure 6.11*a,* but a third generation, a diploid **carposporophyte,** results from the fusion of gametes. **Carpospores,** diploid spores produced by the carposporophyte, develop into sporophytes.

The third type of life history (Fig. 6.11*c*) is perhaps the easiest to understand because it is similar to that of animals, including humans. There is no alternation of generations. Thus, there is only one thallus, and it is diploid. The thallus produces haploid gametes by meiosis. After fertilization the resulting zygote develops into a new diploid thallus. This type of life history is observed in some brown algae (*Fucus* and other rockweeds) and in some green algae (*Codium, Halimeda*).

In the fourth type of life history, which occurs in some green algae (Fig. 6.11*d*), the dominant thallus is haploid and produces haploid gametes. On fertilization the gametes form a diploid zygote. It is in the zygote where meiosis takes place, resulting in haploid spores. Each of these spores develops into a haploid individual, the only kind of thallus in the cycle.

Reproduction in seaweeds is by asexual and sexual means. Sexual reproduction may involve an alternation of a haploid (or gametophyte) and a diploid (or sporophyte) generation.

There are many known variations on these basic life history schemes, and probably others waiting to be discovered. Other aspects of the life history of seaweeds are also interesting. For example, the development of gametes or spores can be influenced by the amounts of nutrients in the water, by temperature, or by day length. High levels of nitrogen nutrients in the water cause the development of asexual spores in sea lettuce, but low levels stimulate the development of gametes instead. The release of gametes and spores can be triggered by the splashing of water in an incoming tide (and therefore by the cycles of the moon) or by chemical messengers received from cells of the opposite sex. In some seaweeds the release of male and female gametes is timed to take place at about the same time.

Economic Importance

People have used seaweeds since time immemorial. Around the world, workers harvest seaweeds to be used in many ways. The most obvious use is as a food source. People from different cultures have discovered that many seaweeds are edible, especially some of the red and brown algae. They are consumed in a variety of ways (see "Seaweeds for Gourmets" p. 111). The farming, or **mariculture,** of seaweed is big business in China, Japan, Korea, and other nations (see Table 17.3, p. 394).

Seaweeds produce several types of gelatinous chemicals, called **phycocolloids,** that are used in food processing and in the manufacture of different products. These phycocolloids are valuable because of their ability to form viscous suspensions or gels even at low concentrations.

One important phycocolloid, **algin** (which comprises alginic acid and its salts, the alginates), is used extensively as a stabilizer and emulsifier in the manufacture of dairy products such as ice cream, cheese, and toppings, which need to be smooth and not likely to separate. Algin is also used in the baking industry to prevent frostings and pies from becoming dry. As a thickener and emulsifier it is used in the pharmaceutical and chemical industries and in the manufacture of various products, from shampoo and shaving cream to plastics and pesticides. Algin also has uses in the making of rubber products, paper, paints, and cosmetics. One of its biggest applications is in the textile industry, where algin thickens the printing paste to provide sharper prints. A major source of algin for commercial uses is the giant kelp (*Macrocystis*). The west coast of temperate North America, particularly California, is home to extensive giant kelp forests, making this an important algin-producing area. The forests are leased from the state of California, and large barges equipped with rotating blades cut and collect the stipes and fronds to a depth of 1 to 2 m (up to 6 ft) below the surface (Fig. 6.12). The stipes quickly grow back toward the surface. Another source of algin is *Laminaria,* which is harvested in the North Atlantic.

A second phycocolloid, **carrageenan,** is obtained from red algae such as Irish moss (*Chondrus*) in the North Atlantic and *Eucheuma* in the tropics. Several species of *Eucheuma* are farmed in the Philippines. Carrageenan is especially valued as an emulsifier. It is used to give body to dairy products and an amazing variety of processed foods, including instant puddings.

Types of cell division:

Mitosis Cell division wherein the resulting cells are identical to the original cell, having their chromosomes in pairs (diploid cells, or 2*n*), as in the case of our body cells.

- Chapter 4, p. 76

Meiosis Cell division wherein the resulting cells are haploid (*n,* or 1*n*), as in the case of gametes (spores in seaweeds), because they contain only half the number of the parent's chromosomes.

- Chapter 4, p. 77

FIGURE 6.12 The *Kelstar,* a kelp harvester based in San Diego, California. It is 55 m (180 ft) long and has a capacity of 600 tons.

Another phycocolloid extracted for its ability to form jellies is **agar.** Agar is used to protect ham, fish, and meats during canning, in low-calorie foods (because it is not digestible by humans), and as a thickener. It is also used in laxatives and other pharmaceuticals and in cosmetics. Biologists use agar as a medium in which to grow bacteria and molds. It is also widely used in research involving the analysis of proteins and DNA. Agar is obtained commercially from several red algae, especially from species of *Gelidium, Gelidiella,* and *Pterocladiella.*

Seaweed can also be used for fertilizer, food additives in animal feeds, and wound dressings in hospitals. Coralline algae are sometimes used in Europe to reduce the acidity of soils. Some red seaweeds are marketed as nutritional supplements.

FLOWERING PLANTS

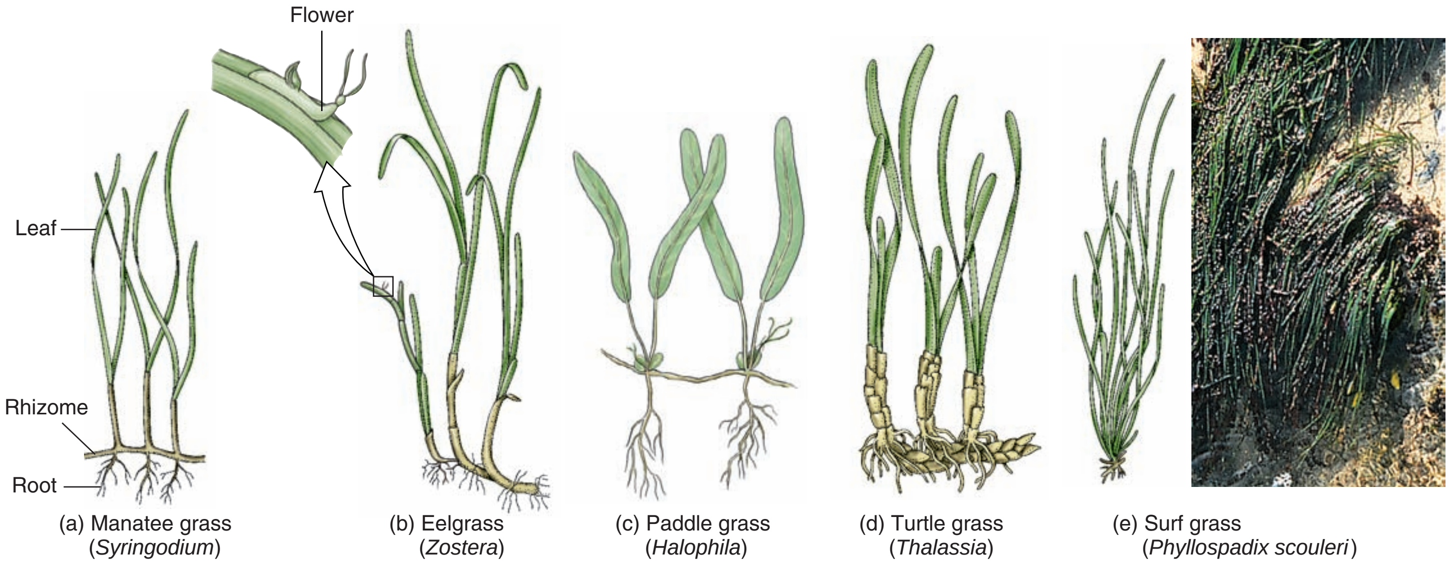
The 250,000 species of **flowering plants,** or **angiosperms** (division **Magnoliophyta**), are the dominant plants on land, but few live in the ocean. Like other land plants (ferns, conifers, and other groups), they have true leaves, stems, and roots, all provided with specialized tissues to transport water, nutrients, and the food manufactured by photosynthesis. As such, they are grouped in the kingdom Plantae. Reproduction involves a dominant sporophyte that features an elaborate reproductive organ, the flower.

Few of these “higher” plants are successful in the oceans. Of all flowering plants, only the seagrasses are truly marine. They often live submerged by seawater, rarely exposed at low tide. Salt-marsh grasses and mangroves inhabit estuaries and shores protected from wave action. They are not completely at home in the ocean, and usually only their roots are covered by water at high tide. There are also many flowering plants adapted to colonize coastal areas exposed to salt-laden winds and occasional sea spray, though they do not tolerate immersion in seawater. Such plants may be found on sand dunes or living along the edges of salt marshes.

Seagrasses

Seagrasses superficially resemble grass but actually are not grasses at all. The closest relatives of certain seagrasses seem to be members of the lily family, so we know that seagrasses evolved from land plants.

Seagrasses have adapted to life in the marine environment. They have horizontal stems called rhizomes that commonly grow beneath the sediment (Fig 6.13). Roots and erect shoots grow from the stems (see Fig. 4.19*b*). Seagrass flowers are typically very small and inconspicuous (see Figs. 6.13*b* and 4.21*d*) because there is no need to attract insects for pollination. The **pollen,**



(a) Manatee grass (*Syringodium*)
(b) Eelgrass (*Zostera*)
(c) Paddle grass (*Halophila*)
(d) Turtle grass (*Thalassia*)
(e) Surf grass (*Phyllospadix scouleri*)

FIGURE 6.13 Some common seagrasses.

Seaweeds for Gourmets

Seaweeds, raw, cooked, or dried, are used as food in many cultures. Seaweeds are good sources of some vitamins and minerals, and some are said to contain substantial amounts of protein. Unfortunately, we cannot digest many of the complex carbohydrates in the plants, but this may be an advantage for those counting calories. Seaweeds can add variety and taste to bland foods and may be used to wrap such foods as rice. Cookbooks containing seaweed recipes have been written to whet the appetites of the most demanding gourmets.

Ulva is not called sea lettuce for nothing. It can be eaten fresh in salads. Seaweeds (or *limu*), including *limu ʻele ʻele* (the green *Enteromorpha prolifera*) and *limu manauea* (the red *Gracilaria coronopifolia*), are beloved by the Hawaiians. Purple laver (a species of *Porphyra,* a red alga) prepared in various ways is still eaten in some parts of the British Isles. It is washed and boiled, then formed into flat cakes, rolled in oatmeal, and fried; it is then called laverbread. Purple laver is also eaten as a hot vegetable or fried with bacon. Irish moss (*Chondrus,* a red alga and a source of carrageenan) is dried and used in preparing *blancmange* and other desserts in eastern Canada, New England, and parts of northern Europe. *Rhodymenia,* another red alga, is dried and eaten, mostly by those living along the Atlantic coasts of Canada and northern Europe. Called *dulse,* it is sometimes still used in making bread and several types of desserts. For those on a diet, dulse can also be chewed like tobacco (of course it's nicotine-free).

It is in the Orient, however, that preparing seaweed for food has reached the level of an art. Several species are carefully cultivated, supporting multimillion-dollar operations. Seaweed culture is a very old tradition in Japan, and Japanese cuisine uses seaweed extensively. Species of *Laminaria* and *Alaria* are dried and shredded, then prepared in various ways. *Laminaria japonica* is heavily cultivated in Japan and when processed is known as *kombu.* The seaweeds are even used to make tea and candy. *Undaria,* or *wakame,* is another edible kelp that is best when fresh or cooked for a very short time. *Porphyra,* a red alga, is used to make thin sheets of *nori,* widely used in soups, and to wrap *sushi,* boiled rice stuffed with bits of raw fish, sea urchin roe, or other ingredients (see Fig. 17.8).

Harvesting kelp (*Laminaria japonica*) in Japan.

Mariculture of edible seaweed is a growing business in many parts of the world (see Table 17.3, p. 394). Seaweeds are harvested by hand, rinsed in water, dried on lines, and sold at health food stores or on the Internet. Connoisseurs use seaweed in salads, soups, omelets, casseroles, and sandwiches. Sea palm (*Postelsia*), also known as "sea noodles," is a best-seller. It is reported to be excellent when sautéed in honey or in butter and garlic. Coastal Indians cooked it in ovens and made it into cakes. Its indiscriminate collection is endangering its survival, which is also true for other edible seaweeds. Pickled bull kelp (*Nereocystis*) tastes even better than regular pickled cucumbers. Bladder rockweed (a type of *Fucus*) makes great tea. Are you ready for feather-boa burgers, French-fried sea palm, and *wakame* shakes?

Seaweed Cake*

1 1/2 cups salad oil
2 cups sugar
3 eggs
2 cups grated or chopped seaweed: bull kelp (*Nereocystis*), *ogo* (*Gracilaria coronopifoloia*), *Eucheuma* (local species from Hawaiʻi), bull kelp or local equivalent
2 cups grated carrots
1 cup crushed, drained pineapple (or 1 cup grated coconut, preferably fresh)
2 1/2 cups flour
1 teaspoon baking soda
1 teaspoon salt
1 teaspoon cinnamon
1 cup chopped walnuts (optional)

Mix well the sugar and salad oil. Add the eggs, one at a time, beating well after each egg is added. Add the seaweed, carrots, and pineapple (or coconut). Sift together the flour, baking soda, salt, and cinnamon and add to mixture; mix well. Add the chopped walnuts if desired. Bake in oblong or bread-loaf pan at 160°C (350°F) for 45 to 50 minutes. Cake may be covered with buttercream frosting. Enjoy.

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*Adapted from I. A. Abbot, *Limu, An Ethnobotanical Study of Some Hawaiian Seaweeds,* 4th edition, National Tropical Botanical Garden, Lawaʻi, Kauaʻi, Hawaiʻi, 1996.

which contains the sperm, is carried instead by water currents. It is often released in strands. In some seagrasses the pollen grains are long and thread-like instead of tiny and round, as in land plants. Tiny seeds, which in some species develop inside small fruits within the flower, result from successful fertilization. These seeds are dispersed by water currents and perhaps in the feces of the fish and other animals that browse on the plants.

Eelgrass (*Zostera*) is the most widely distributed of the nearly 60 species of seagrasses known. It is found in many temperate and tropical regions of the world, where it inhabits shallow, well-protected coastal waters such as bays and estuaries (see Fig. 13.15). It has distinctively flat, ribbon-like leaves (see Figs. 6.13*b* and 13.17). It is common in oxygen-poor sediments. Thick *Zostera* beds are highly productive and provide shelter and food to a variety of animals, some of considerable economic importance. Surf grass (*Phyllospadix;* see Fig. 6.13*e*) is an unusual seagrass because it is an inhabitant of rocky coasts exposed to wave action, as its common name implies. Some species may become exposed at low tides. It is found on the Pacific coast of North America.

More information on the biology and ecological significance of seagrasses is given in "Seagrass Beds," p. 290.

Salt-Marsh Plants

Cordgrasses (*Spartina;* see Fig. 12.7) are true members of the grass family. They are not really marine species but, rather, land plants tolerant of salt. Unlike seagrasses, which are true marine species, cordgrasses do not tolerate total submergence by seawater. They live in salt marshes and other soft-bottom coastal areas throughout temperate regions. Cordgrass salt marshes are highly productive and provide habitat and breeding grounds for many species important to fisheries. They also offer protection against erosion and provide natural water purification systems (see Fig. 18.5).

Cordgrasses inhabit the zone above mudflats that becomes submerged by seawater only at high tide, so their leaves are always partly exposed to air. Salt glands in the leaves excrete excess salt. Other salt-tolerant plants, or **halophytes,** such as pickle weed (*Salicornia;* see Fig. 12.8), may be found at higher levels on the marsh. Salt-marsh plants and their adaptations to the estuarine environment along the mouths of rivers are discussed in "Salt Marshes" (p. 274).

Mangroves

Mangroves are trees and shrubs adapted to live along tropical and subtropical shores around the world. They are essentially land plants that can tolerate salt. Luxuriant and very productive mangrove forests flourish along muddy or sandy shores protected from waves (Fig. 6.14).

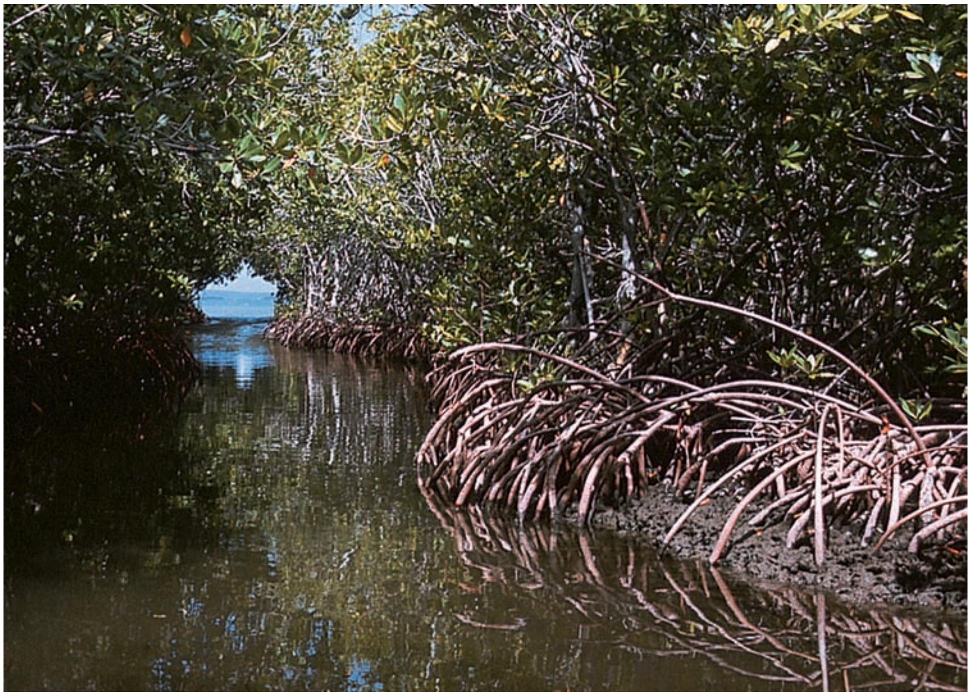
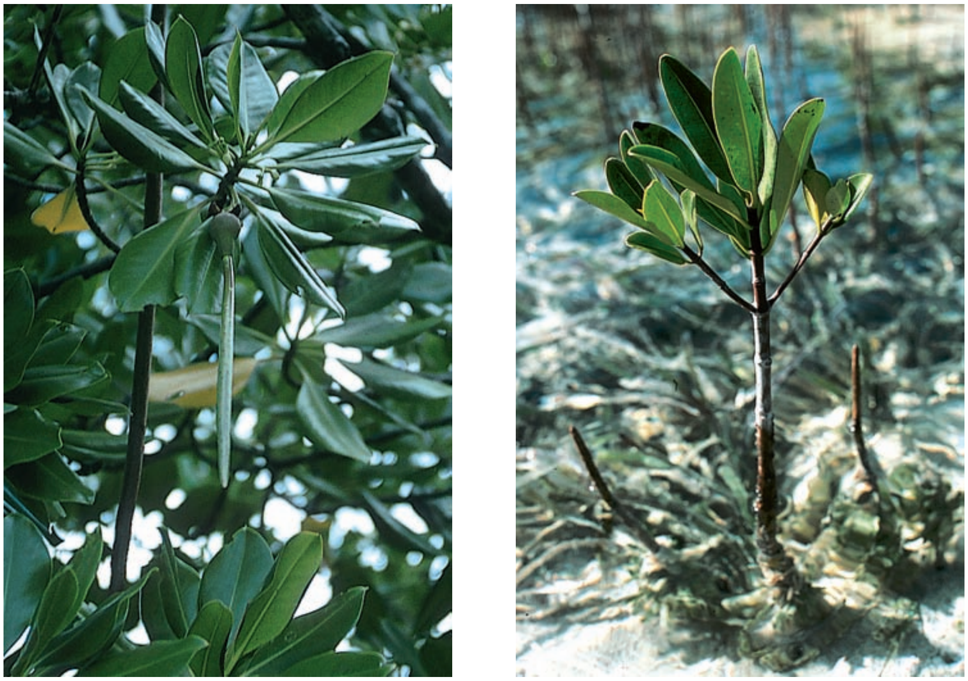


FIGURE 6.14 The red mangrove (*Rhizophora mangle*) forms lush forests along shores in Florida, the Caribbean, the Gulf of California, and other tropical regions of the Western Hemisphere and West Africa. Notice the long roots extending into the mud, exposed here at low tide. Other species of mangroves can be found farther inland (see Fig. 12.18).



(a) (b)

FIGURE 6.15 A seedling of the red mangrove (*Rhizophora mangle*) (*a*) as it appears in the tree and (*b*) one that has taken root in the soft sediment.

Mangroves include at least 80 mostly unrelated species of flowering plants. They are adapted in various ways to survive in a salty environment where water loss from leaves is high and sediments are soft and poor in oxygen. Adaptations become more crucial in mangroves living right on the shore, such as species of the red mangrove (*Rhizophora*), which are found throughout the tropics and subtropics. The extreme northern and southern limits of the red mangrove are those areas in which killing frosts begin. Salt marshes replace red mangrove forests in areas exposed to frosts.

The leaves of the red mangrove are thick, an adaptation to reduce water loss. As in several other mangroves, seeds germinate while still attached to the parent tree (Fig. 6.15*a*). They develop into elongated, pencil-shaped seedlings as long as 30 cm (1 ft) before falling from the parent. Successful seedlings stick in the soft, muddy sediment like a knife thrown into a lawn, or float in the water to be carried by currents to new locations (Fig. 6.15*b*). The types and distribution of mangroves and their significance in the marine environment are discussed in "Mangrove Forests" (p. 276).

> Flowering plants, dominant on land, have few marine representatives. Seagrasses, which are true marine species, and salt-tolerant plants like salt-marsh plants and mangroves are exceptions. They have successfully adapted to soft-bottom coastal regions, developing as highly productive meadows and, in the case of mangroves, forests along the shore.

Table 6.1 Most Important Characteristics of Seaweeds and Marine Plants

Group	**Distinguishing Features**	**Photosynthetic Pigments**	**Major Food Reserves**	**Major Cell-Wall Components**	**Significance in the Marine Environment**
Green algae	Eukaryotic, unicellular and multicellular; mostly bottom-dwelling	Chlorophyll *a*, *b*, carotenoids	Starch	Cellulose; calcium carbonate in calcareous algae	Primary producers; calcareous algae are important sources of calcareous deposits in coral reefs
Brown algae	Eukaryotic, multicellular; bottom-dwelling	Chlorophyll *a*, *c*, carotenoids (flucoxanthin and others)	Laminarin, oil	Cellulose; alginates	Primary producers; dominant components of kelp forests
Red algae	Eukaryotic, multicellular; bottom-dwelling	Chlorophyll *a*, phycobilins (phycocyanin, phycoerythrin), carotenoids	Starch	Agar, carageenan, cellulose, calcium carbonate in coralline algae	Primary producers; coralline algae are important sources of calcareous deposits in coral reefs
Flowering plants	Eukaryotic, multicellular; bottom-dwelling	Chlorophyll *a*, *b*, carotenoids	Starch	Cellulose	Dominant primary producers in seagrass beds, salt marshes, and mangrove forests; nursery grounds for many species; help stabilize soft bottoms, protect coast from turbulence

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Some biologists place the seaweeds in the kingdom Plantae; others consider seaweeds to be protists. Assume that a better arrangement is to group the green, brown, and red algae in their own kingdom, which we will call Macrophyta. Characterize the new kingdom by first giving its unique characteristics and then differentiate it from the protists and the true plants. Be sure to consider major exceptions or overlaps.
2. Only very few flowering plants have invaded the oceans, but those that have are very successful. What are some possible reasons for the small number of marine flowering plants? How do those that have taken the step manage to thrive in some environments?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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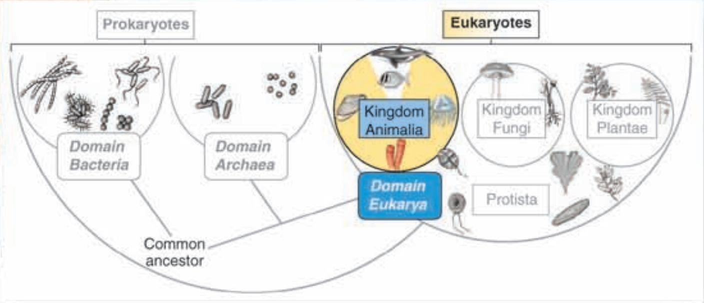
The crab *Trapezia flavopunctata* and its coral host, *Pocillopora*.

7 CHAPTER

Marine Animals Without a Backbone



Most species of multicellular organisms inhabiting our planet are **animals** (kingdom **Animalia**). In contrast to photosynthetic organisms like algae and plants, we animals cannot manufacture our own food and must therefore obtain it from others. The need to eat has resulted in the evolution of myriad ways of obtaining and processing food, as well as equally diverse ways of avoiding being eaten.

The colorful crab in the photo on this page is a good example. It inhabits reef-building corals, relying on them for food and shelter. The crabs feed on mucus, which the coral produces to keep its surface free from debris. The coral is also an animal, though it may not look like one. It gets some of its food from **zooxanthellae** that live in its tissues. The coral also eats small planktonic organisms that it captures by using stinging structures in its tentacles. Though an absent-minded crab is occasionally captured by a fish or an octopus, the crabs are usually safe among the coral branches. The crabs repay the favor by using their claws to drive away other animals that have a taste for coral tissue.

Our survey of the many kinds of marine animals follows the traditional classification into two major groups: the **vertebrates,** which have a **backbone** (a row of bones called **vertebrae**), and the **invertebrates,** animals without a backbone.

At least 97% of all species of animals are invertebrates. All major groups of invertebrates have marine representatives, and many are exclusively marine. Only a few groups have successfully invaded land. Were it not for one of these groups, the insects, we could boast without hesitation that most invertebrate species, and therefore most animals, are marine.

Zooxanthellae Dinoflagellates (single-celled algae) that live within animal tissues.
• Chapter 5, p. 96 Figure 14.1

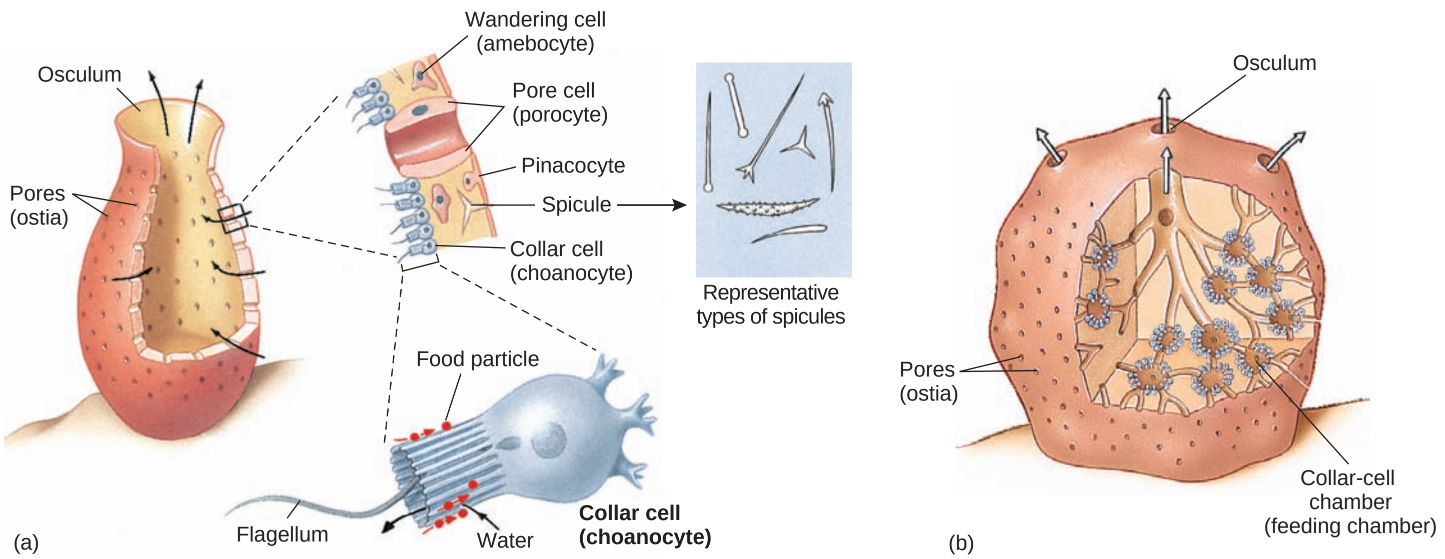


FIGURE 7.1 Sponges consist of complex aggregations of cells that carry out specific functions. Collar cells trap food particles in both (*a*) simple and (*b*) complex sponges.

SPONGES

Sponges are best described as aggregations of specialized cells. Sponges have a cellular level of organization, meaning that the cells are largely independent of each other and do not form true **tissues** and **organs** (see Table 7.1, p. 148). Sponges are among the structurally simplest multicellular animals (see Fig. 7.54).

Nearly all sponges are marine. All are **sessile,** living permanently attached to the bottom or some other surface. They show an amazing variety of shapes, sizes, and colors but share a relatively simple body plan. Numerous tiny pores, or **ostia,** on the surface allow water to enter and circulate through a series of canals where **plankton** and organic particles are filtered out and eaten (Fig. 7.1*a*). This network of canals and a relatively flexible skeletal framework give most sponges a characteristic spongy texture. Because of this unique body plan, sponges are classified as the phylum **Porifera,** or "pore bearers."

Sponges may be similar to the first multicellular animals, which were probably simple colonies in which some cells became specialized for such functions as feeding and protection. Sponge cells are very plastic and easily change from one type to another. If experimentally separated, the cells can even regroup and form a new sponge (Fig. 7.2).

The architecture of sponges is best understood by examining the simplest kind of sponge (Fig. 7.1*a*). The outer surface is covered with flat cells called **pinacocytes** and occasional tube-like **pore cells,** or **porocytes,** through which a microscopic canal allows water to enter. Water is pumped into a larger feeding chamber lined with **collar cells,** or **choanocytes.** Each choanocyte has a flagellum that creates currents and a thin collar that traps food particles, which are then ingested by the body of the cell. Water then leaves through the **osculum,** a large opening on top of the sponge.

Sponges are an example of **suspension feeders,** animals that eat food particles suspended in the water. Because sponges actively filter the food particles, they are a type of suspension feeder known as **filter feeders** (Fig. 7.3). In contrast, **deposit feeders** eat **detritus** that settles on the bottom.

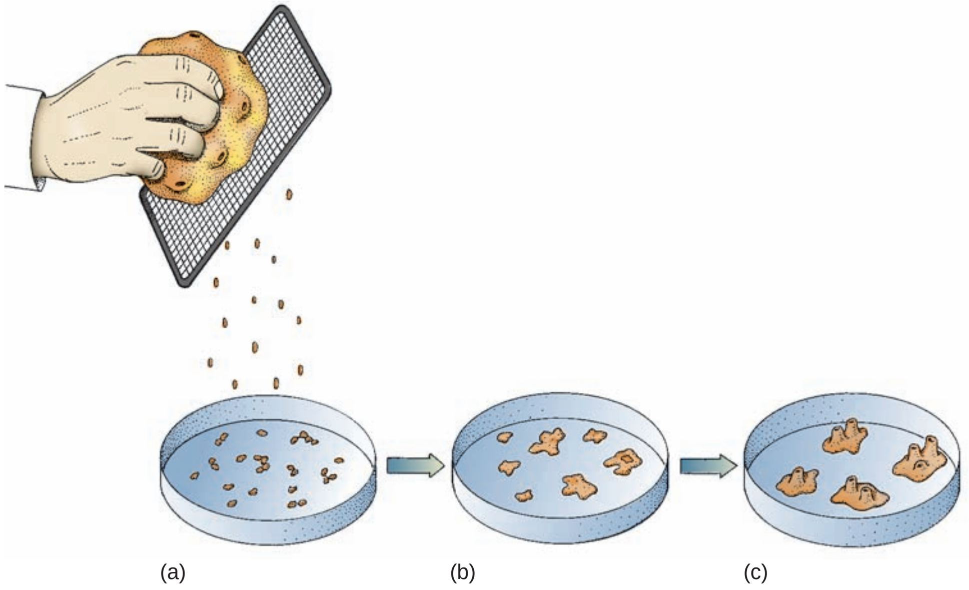


FIGURE 7.2 Some sponges form new individuals after their cells are separated from one another. The cells can be separated by squeezing pieces through a very fine sieve (*a*). In a matter of hours, the cells begin to aggregate and reorganize (*b*) and eventually form new sponges (*c*). When cells of different species are mixed, they generally reaggregate into their individual species.

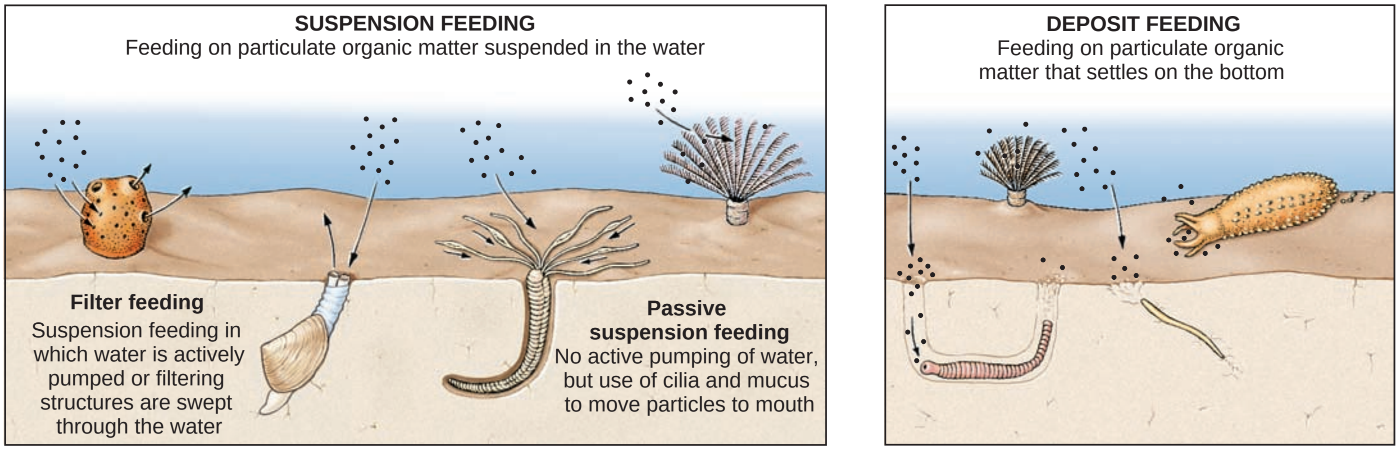

SUSPENSION FEEDING
Feeding on particulate organic matter suspended in the water
Filter feeding
Suspension feeding in which water is actively pumped or filtering structures are swept through the water
Passive suspension feeding
No active pumping of water, but use of cilia and mucus to move particles to mouth
DEPOSIT FEEDING
Feeding on particulate organic matter that settles on the bottom

FIGURE 7.3 Feeding on particulate organic matter can be classified as suspension or deposit feeding. The difference between these two types of feeding is not always well defined. Fanworms, for instance, are tube-dwelling polychaetes that switch back and forth between suspension and deposit feeding, depending on the strength of the water current.

Most marine sponges show a more complex arrangement in which the collar cells are restricted to chambers connected to the outer pores by a network of canals (Fig. 7.1*b*). Water exits not through a single osculum but through several oscula, each of which serves as the exit for many canals. This increased complexity is associated with increased size, which demands higher water flow through the sponge and therefore a larger surface area of collar cells.

Sponges are among the structurally simplest multicellular animals, lacking true tissues and organs. They are mostly marine, living as attached filter feeders.

As sponges get larger, they need structural support. Most have **spicules,** transparent **siliceous** or **calcareous** supporting structures of different shapes and sizes (Fig. 7.1*a*). Many also have a skeleton of tough, elastic fibers made of a protein called **spongin.** Spongin may be the only means of support, or it may be found together with spicules. When present, spongin and spicules are mostly between the outer and inner layers of cells. Wandering cells, or **amebocytes,** secrete the spicules and spongin. Some of these wandering cells also transport and store food particles. Some can even transform themselves into other types of cells, quickly repairing any damage to the sponge.

Many sponges reproduce **asexually** when branches or buds break off (see Fig. 4.19*a*) and grow into separate sponges identical to the original one. Sponges also reproduce **sexually** by producing **gametes.** Unlike most animals, sponge gametes are not produced by **gonads.** Instead, specialized collar cells or amebocytes develop into gametes (Fig. 7.4). The gametes are like those of other animals: large, nutrient-rich eggs and smaller sperm cells that have a flagellum. Most sponges are **hermaphrodites,** animals in which individuals have both male and female gonads. Some species, however, have separate males and females, which is the case in many other invertebrates. Sponges typically release sperm into the water. The release of gametes into the water is called **broadcast spawning.** The eggs, however, are usually retained inside the body and fertilization takes place internally after sperm enter the sponge.

The early stages of development take place inside the sponge. Eventually, a tiny, flagellated sphere of cells is released into the water (Fig. 7.4). This planktonic **larva,** called the parenchymula larva in most sponges, is carried by currents until it settles on the bottom and develops into a minute sponge. Most marine invertebrates have characteristic larvae that eventually change into juveniles that resemble adults. This drastic change from the larva to the adult is called **metamorphosis** (Fig. 7.4).

Almost all the approximately 6,000 known species of sponges are marine. Sponges live from the poles to the tropics, but the largest number of species inhabits shallow tropical waters. Sponges may grow into branching, tubular (Fig. 7.5*a*), round, or volcano-like masses that sometimes reach a huge size. **Encrusting** sponges form thin, sometimes brightly colored growths on rocks or dead coral (Fig. 7.5*b*).

Glass sponges, such as the Venus flower basket sponge (*Euplectella*), live anchored in deep-water sediments and have a lace-like skeleton of fused siliceous spicules. **Boring sponges** (*Cliona*) bore thin channels through calcium carbonate, such as oyster shells

Tissues Specialized, coordinated groups of cells.
Organs Structures consisting of several types of tissues grouped together to carry out particular functions.
- Chapter 4, p. 70

Plankton Organisms that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

Siliceous Made of silica (SiO_2).
Calcareous Made of calcium carbonate ($CaCo_3$).
- Chapter 2, p. 32

Gametes Specialized reproductive cells with half the genetic complement of each parent, usually produced by organs called *gonads: sperm* (male gametes produced by the *testes*) and *eggs* (female gametes produced by the *ovaries*).
- Chapter 4, p. 77

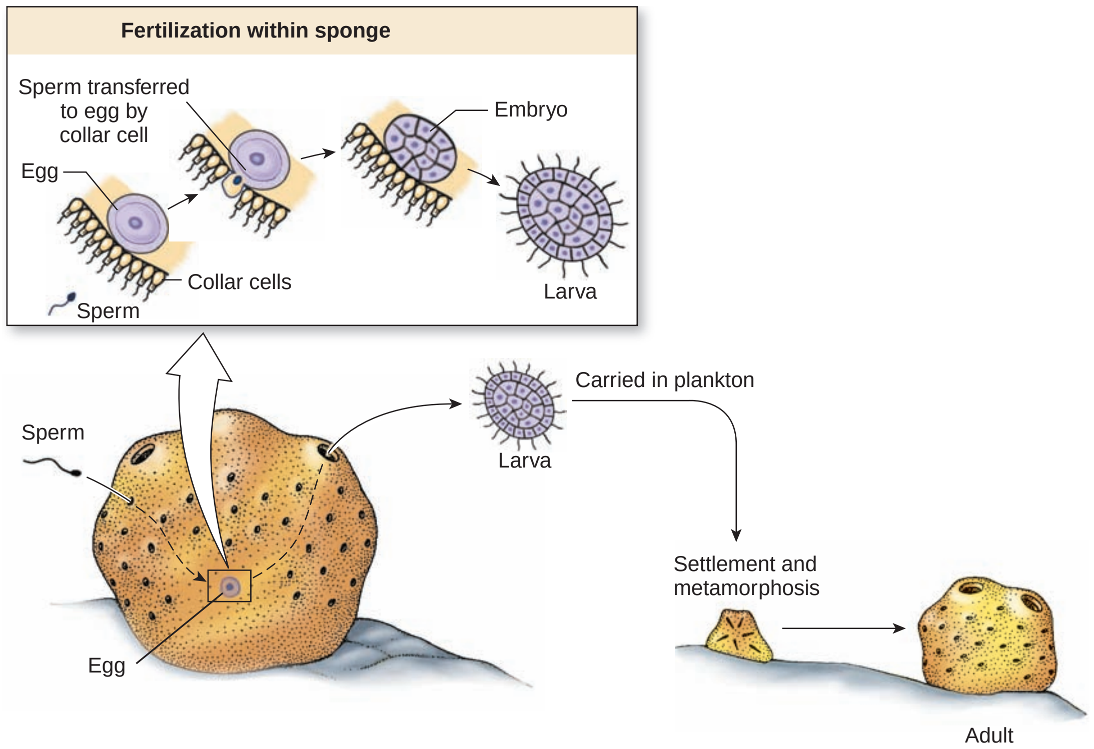

Fertilization within sponge
Sperm transferred to egg by collar cell
Egg
Embryo
Collar cells
Sperm
Larva
Carried in plankton
Sperm
Larva
Settlement and metamorphosis
Egg
Adult

FIGURE 7.4 Sexual reproduction in many marine sponges involves fertilization within the sponge, development of the embryo into a larva, the release of a planktonic larva, and its eventual settlement and metamorphosis into a new sponge on the bottom.

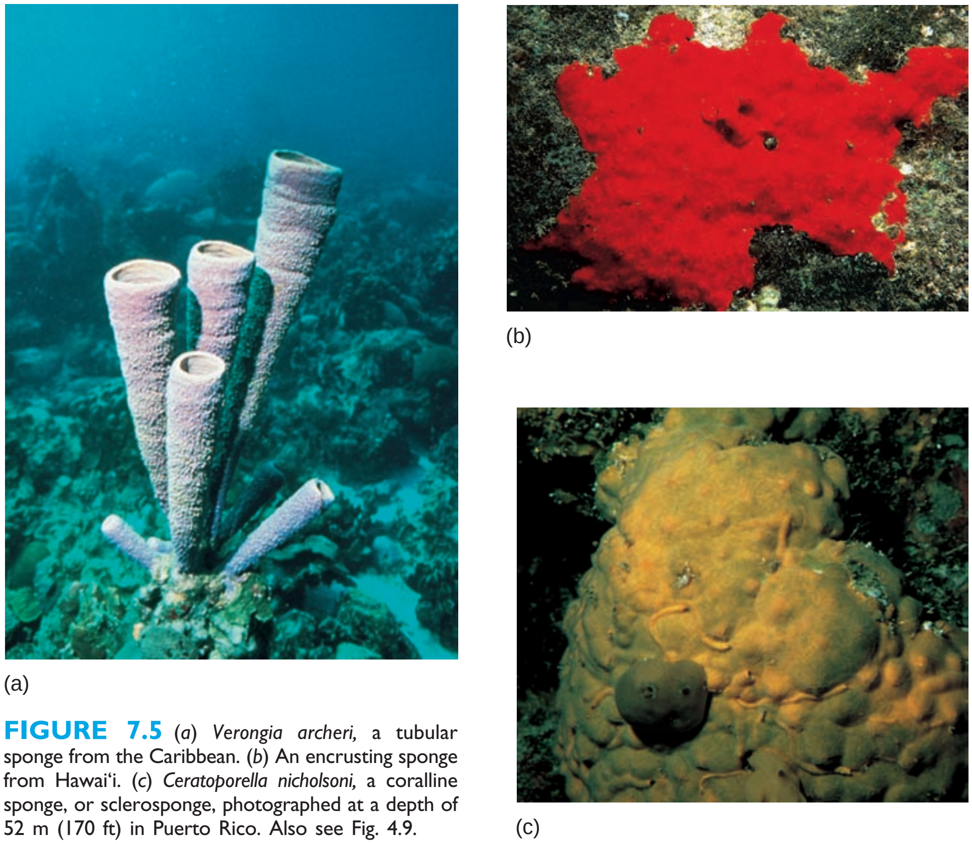


FIGURE 7.5 (*a*) *Verongia archeri,* a tubular sponge from the Caribbean. (*b*) An encrusting sponge from Hawai'i. (*c*) *Ceratoporella nicholsoni,* a coralline sponge, or sclerosponge, photographed at a depth of 52 m (170 ft) in Puerto Rico. Also see Fig. 4.9.

and corals. In the **sclerosponges,** or **coralline sponges** (*Ceratoporella;* Fig. 7.5*c*), a calcium carbonate skeleton forms beneath the body of the sponge, which also contains siliceous spicules and spongin. Sclerosponges were first known as fossils, but living specimens were discovered in underwater caves and on steep coral reef slopes after the advent of scuba diving.

Some marine sponges are of commercial importance. Bath sponges (*Spongia*) are still harvested in a few locations in the Gulf of Mexico and the eastern Mediterranean in what remains of a once-flourishing industry. Bath sponges, not to be confused with synthetic sponges, consist of the spongin fibers remaining after cells and debris are washed away. Some marine sponges produce potentially useful chemicals (see "Take Two Sponges and Call Me in the Morning," p. 397).

CNIDARIANS: RADIAL SYMMETRY

The next level of organizational complexity among animals after the sponges involves quite a big step: the evolution of multicellular animals with tissues that perform specific functions. This development makes it possible for organisms to swim, respond to external stimuli, and engulf prey, among other things. **Cnidarians,** sometimes called **coelenterates** (phylum **Cnidaria**), include the sea anemones, jellyfishes, corals, and their relatives.

Besides having a tissue level of organization, cnidarians display **radial symmetry,** where similar parts of the body are arranged and

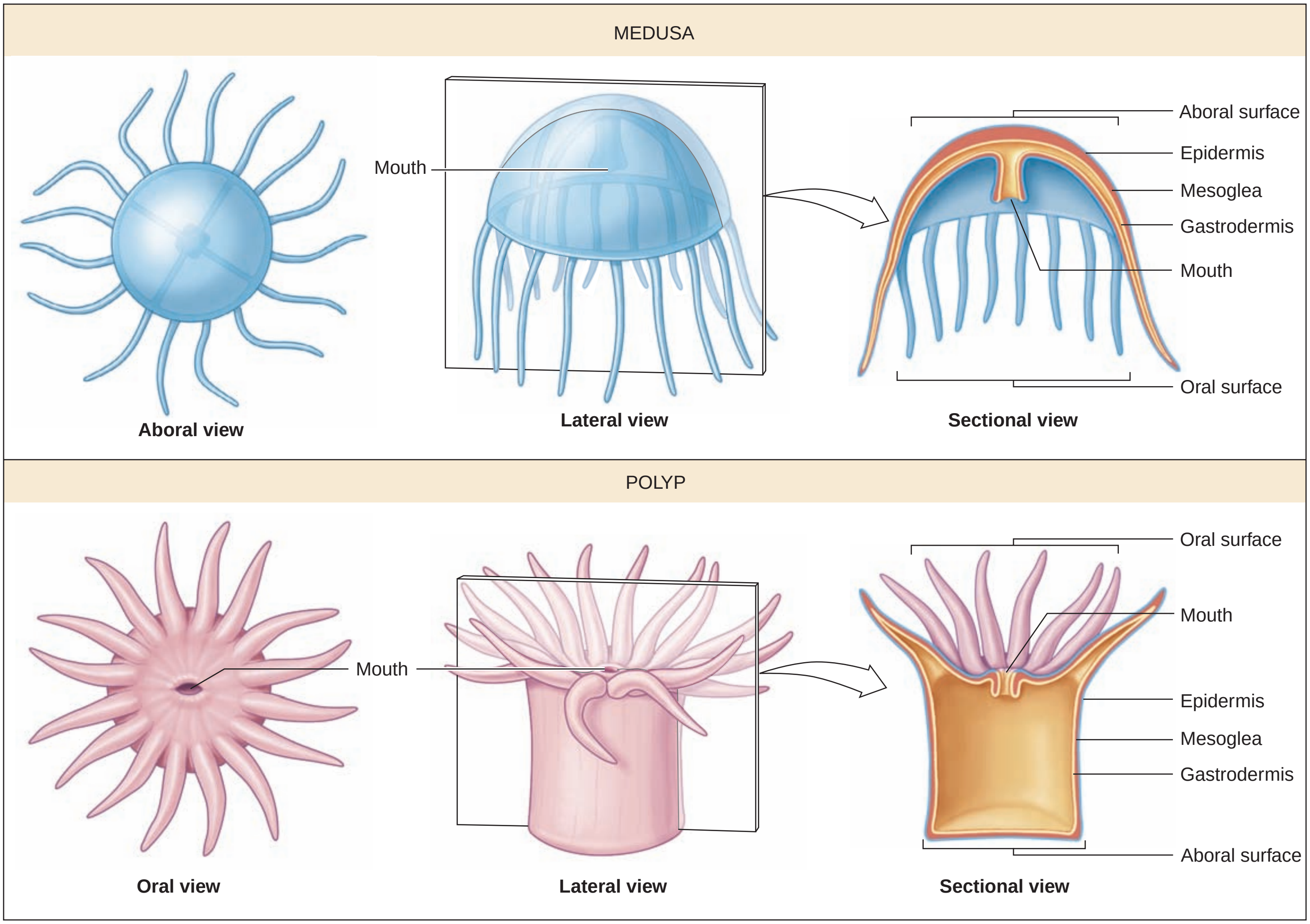


FIGURE 7.6 The flower-like appearance of many cnidarians is a consequence of their radial symmetry. In both the medusa and polyp, tentacles are arranged and repeated around a central axis that runs through the mouth.

repeated around a central axis (Figs. 7.6 and 7.13*a*). If a radially symmetrical animal were cut like a pizza, all the resulting slices would be similar. Animals with radial symmetry look the same from all sides and have no head, front, or back. They do, however, have an **oral surface,** where the mouth is, and an **aboral surface** on the opposite side (Fig. 7.6).

Cnidarians have a centrally located mouth surrounded by **tentacles,** slender, finger-like extensions used to capture and handle food. The mouth opens into a **gut,** where food is digested. The cnidarian gut is a blind cavity with only one opening, the mouth. Cnidarians capture small prey by discharging their **nematocysts** (or cnidae), unique stinging structures found within **cnidocytes,** specialized cells in the tentacles (see Fig. 7.8).

Cnidarians occur in two basic forms (Fig. 7.6): a **polyp,** a sac-like attached stage with the mouth and tentacles oriented upward, and a bell-like **medusa,** or jellyfish, which is like an upside-down polyp adapted for swimming. The life history of some cnidarians includes both polyp and medusa stages. Others spend their entire lives as either polyp or medusa.

The characteristic larva of most cnidarians is the **planula,** a cylindrical, ciliated stage consisting of two layers of cells. After a time in the plankton, the planula settles on the bottom and metamorphoses into a polyp or develops into a medusa.

The radially symmetrical cnidarians have unique stinging structures, nematocysts, that are used to capture prey. Cnidarians exist as either polyps or medusae, or both in alternation. Most have a planula larva.

Two layers of cells form the body wall of cnidarians. One of these, the **epidermis** (see Figs. 7.6 and 7.9), is external, whereas the other, the **gastrodermis,** lines the gut. There is also a narrow, gelatinous middle layer, or **mesoglea,** that usually doesn't contain cells. In medusae this layer is expanded to form a gelatinous, domed bell, hence their common name of jellyfish.

Types of Cnidarians

The basic cnidarian body plan, though structurally simple, has been very successful. Some 10,000 species are known, almost all of which are marine.

Hydrozoans The **hydrozoans** (class **Hydrozoa**) have a wide range of forms and life histories. Many consist of feathery or bushy colonies of tiny polyps. They attach to pilings, shells, seaweeds, and other surfaces (Fig. 7.7). The polyps may be specialized for feeding, defense, or reproduction.

Reproductive polyps produce minute, transparent medusae (Fig. 7.8). These medusae, usually planktonic, release gametes into the water. The fertilized eggs develop into free-swimming planula larvae. Each planula settles on the bottom and develops into a polyp. This first polyp divides repeatedly and develops into a colony of many interconnected polyps. There are, however, several variations of this life cycle. For instance, some hydrozoans lack a polyp stage, and instead their planula develops into a medusa. A few lack a medusa stage, and instead the polyp produces gametes directly.

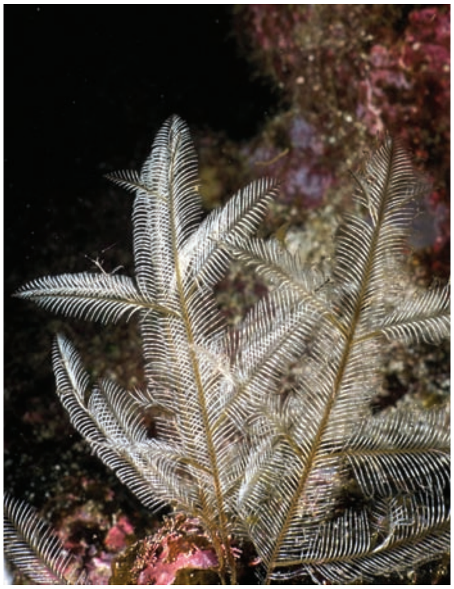
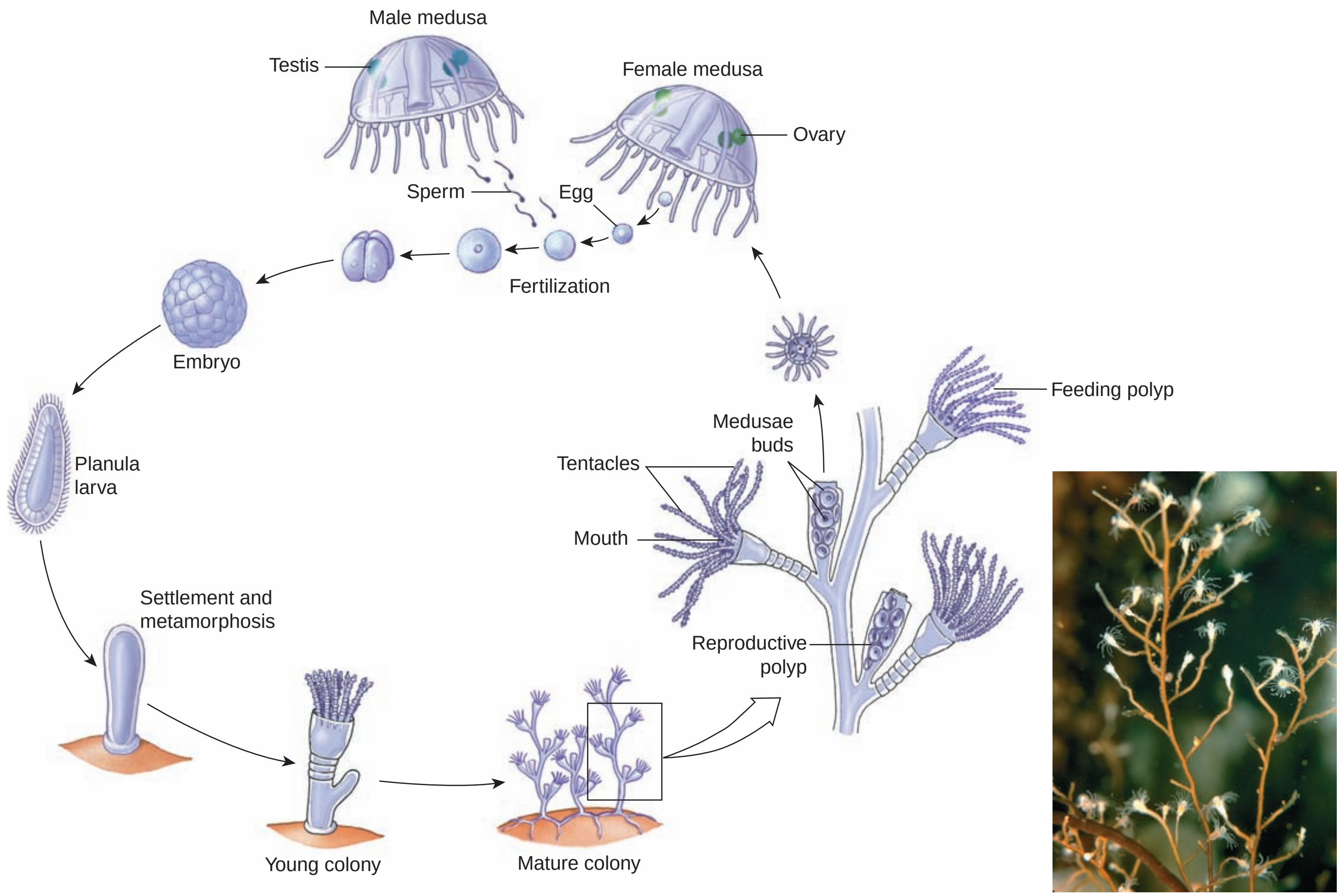


FIGURE 7.7 Colonial hydrozoans include this feather-like colony of the hydroid *Macrorhynchia phillipina.* It is a common species in warm and some temperate waters around the world.

Siphonophores are hydrozoans that form drifting colonies of polyps. Some polyps in a siphonophore colony may be specialized as floats, which may be gas-filled, as in the Portuguese man-of-war (*Physalia physalis;* Fig. 7.9), or contain droplets of oil. Other siphonophore polyps form long tentacles used to capture prey. Toxins from the nematocysts can produce painful reactions in swimmers or divers.

Scyphozoans The larger jellyfishes common in all oceans are quite different from the often tiny hydrozoan medusae. These large medusae (Fig. 7.10) are the dominant stage of the life cycle of **scyphozoans** (class **Scyphozoa**). The polyps of scyphozoans are very small and release juvenile medusae. A few species lack a polyp stage altogether. The rounded body, or **bell,** of some scyphozoan medusae may reach a diameter of 3 m (10 ft) across in a recently discovered



Life Cycle of a hydrozoan

Eudendrium, worldwide

FIGURE 7.8 The life cycles of hydrozoans follow different patterns. A common one involves a sessile, asexually reproducing colony of polyps that releases planktonic, sexually reproducing medusae.

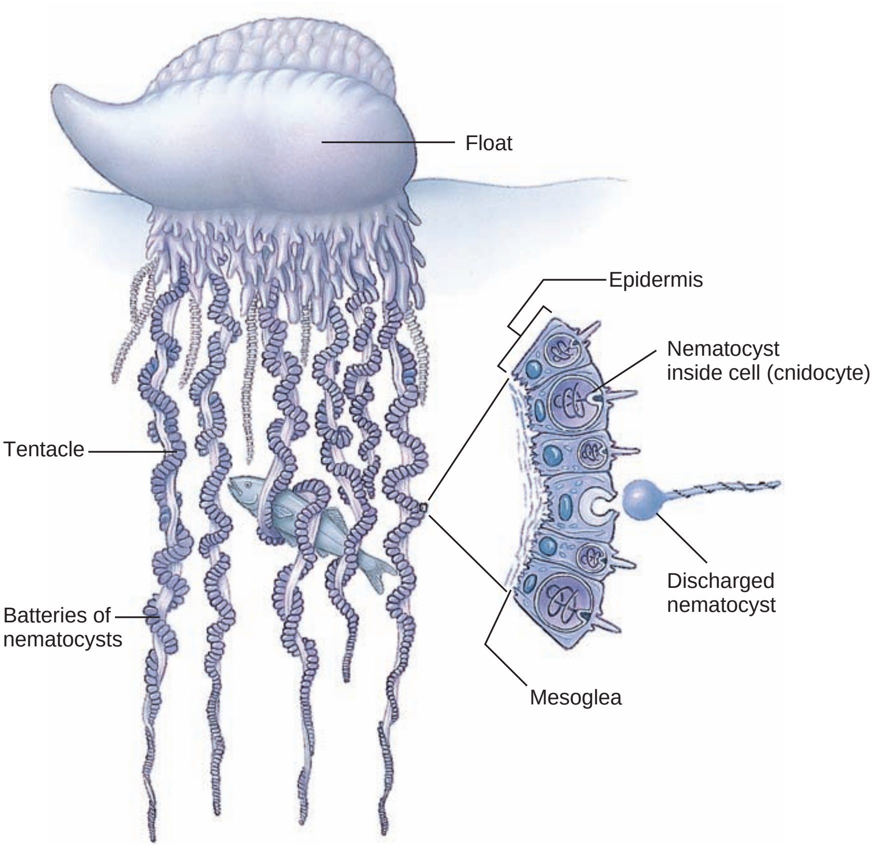


FIGURE 7.9 A diagrammatic representation of the Portuguese man-of-war (*Physalia physalis*). It consists of a colony of specialized polyps, one of which forms a gas-filled float that may reach 30 cm (12 in) in length. The long tentacles, here contracted, are armed with nematocysts notorious for their ability to sting swimmers.

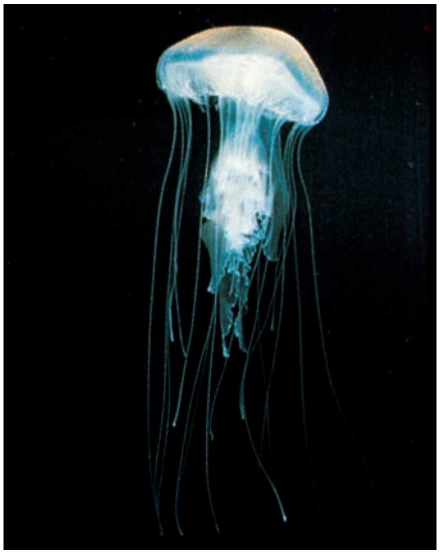


FIGURE 7.10 Scyphozoan medusae are larger and more complex than hydrozoan medusae. This example is the sea nettle (*Chrysaora quinquecirrha*), which is found from Cape Cod to the Gulf of Mexico. It is especially common in Chesapeake Bay.

deep-water species. Scyphozoans swim with rhythmic contractions of the bell, but their swimming ability is limited and they are easily carried by currents. Some scyphozoan medusae are among the most dangerous marine animals known, giving extremely painful and sometimes fatal stings. This is particularly true of cubomedusae, once classified as scyphozoans but now placed in their own group, the class **Cubozoa** (see "The Case of the Killer Cnidarians," p. 122).

Anthozoans Most cnidarian species are **anthozoans** (class **Anthozoa**), solitary or colonial polyps that lack a medusa stage. The anthozoan polyp is more complex than hydrozoan or scyphozoan polyps. The gut, for instance, contains several thin partitions, or **septa** (see Fig. 14.2), which provide additional surface area for the digestion of large prey. Septa also provide support, which allows the polyp to be larger than the polyps of other cnidarians. **Sea anemones** are common and colorful anthozoans that often have large polyps (see Fig. 11.26). Colonial anthozoans occur in an almost infinite variety of shapes. **Corals** include various groups of mostly colonial anthozoans (see Table 14.1, p. 304). Many of these have calcium carbonate skeletons and, though such corals occur in cold waters, in tropical waters they often form **coral reefs. Gorgonians,** such as sea fans (Fig. 7.11), are colonial anthozoans that secrete a tough, branching skeleton made in part of protein. **Precious corals** are gorgonians with fused red or pink calcareous spicules in addition to the protein skeleton. **Black corals,** which are neither gorgonians nor stony corals, secrete a hard, black, protein skeleton. Both precious and black corals are carved into jewelry. Some anthozoans form fleshy colonies with large polyps and no hard skeletons. Examples of these are the soft corals, sea pens (see Fig. 13.13), and sea pansies.

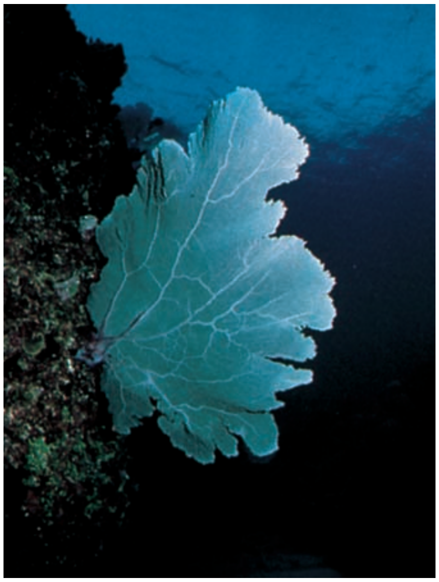


FIGURE 7.11 Sea fans are gorgonians with branches that grow in only one plane and have many cross-connections.

Biology of Cnidarians

The presence of tissues allows cnidarians to perform more complex functions than sponges can. In particular, cnidarians display advances in feeding and can sense and respond to their environment.

Feeding and Digestion Practically all cnidarians are **carnivores,** animals that prey on other animals. Many capture and digest prey much bigger than that of filter feeders such as sponges. Cnidarians use their nematocysts primarily to capture prey. Each nematocyst consists of a fluid-filled capsule containing a thread that can be quickly ejected (see Fig. 7.9). The thread may be sticky or armed with spines, or it may be a long tube that wraps around parts of the prey. Some nematocysts contain toxins.

The Case of the Killer Cnidarians

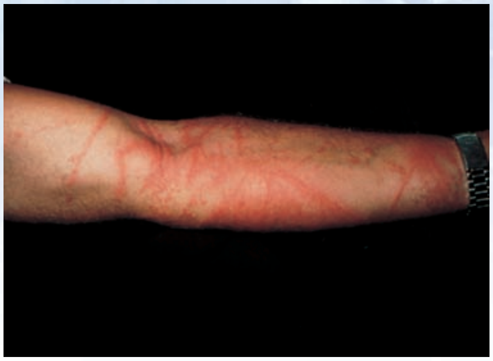
The stings of most cnidarians are harmless to humans, but there are exceptions. Delicate and innocent-looking, some cnidarians are among the most dangerous marine animals. The sinister side of these creatures is due to the potent toxins released by their nematocysts.

The Portuguese man-of-war (*Physalia*), a siphonophore, is found in warm waters around the world. Though its blue, sail-like float can be seen fairly easily, its long tentacles are nearly invisible. Armed with thick batteries of nematocysts, these tentacles may reach 50 m (165 ft) in length. Portuguese men-of-war may occur by the thousands, sometimes forcing the closure of beaches. Pieces of tentacle that wash ashore can be as nasty as the whole animal.

Physalia stings are very painful, like being repeatedly burned with a hot charcoal. The pain may last for hours, especially if sensitive areas of the body are affected. Red lines appear wherever tentacles have touched the skin, and welts usually follow. Both of the authors have had encounters with *Physalia*, painful but fortunately less severe than the experiences of others. One of us saw a man get stung on the hand. When the wave of intense pain reached his armpit, the man passed out. Even more severe reactions may occur. There can be nausea and difficulty in breathing. Contact of tentacles with the eye may damage the cornea. Allergic reactions to the toxin may cause shock and even death, and swimmers may drown because of pain or shock.

If you are stung, the best thing to do is not to panic. Carefully wash the area with seawater, but don't rub the area or wash with fresh water because this stimulates firing of the nematocysts. Vinegar and alcohol will inactivate the nematocysts. Urine may be useful if nothing else is available. The toxin is a protein, and some recommend papain, a protein-digesting enzyme found in meat tenderizer. The meat tenderizer is of little help, however, because the poison is injected into the skin while the meat tenderizer remains on the surface. Severe reactions should be treated in a hospital.

A group of medusae, the cubomedusae, release even more powerful toxins. The sea wasp, or box jellyfish, *Chironex fleckeri*, of northern Australia, Southeast Asia, and the Indian Ocean, has been responsible for many known deaths. Its stings cause immediate, extreme pain. Death due to heart failure may follow within minutes, especially in children. Skin that touches the tentacles swells up, and the purple or dark brown lines that are left are slow to heal. Fortunately, an antivenin ("antivenom") has been developed. Otherwise, the recommended first aid is to dowse the sting with vinegar.



The sting of *Chiropsalmus,* a cubomedusa.

There are other tropical cubomedusae that give severe stings, particularly in Australia and the West Indies. The irukandji (*Carukia barnesi*) of northern Australia have caused several deaths in recent years. Unlike the sea wasp, irukandji normally live offshore but currents occasionally sweep them into shallow water.

Cubomedusae are more common along the shore during summer. Their transparent, almost square bells are difficult to see in the water. Most are small, but in the sea wasp the bell may reach 25 cm (almost 10 in) in diameter, and the tentacles may stretch to 4.5 m (15 ft). Irukandji have a bell only 2.5 cm (1 in) in diameter and four tentacles of about the same length, so they are almost impossible to spot in the water.

After ingestion, food passes into the gut, where it is digested. The initial phase of digestion is said to be **extracellular** because it takes place outside cells. **Intracellular digestion** within cells lining the gut completes the breakdown of food.

Behavior Though cnidarians lack a brain or true nerves, they do have specialized **nerve cells.** These cells interconnect to form a **nerve net** that transmits impulses in all directions. This simple nervous system can produce some relatively sophisticated behaviors. Some anemones can tell whether other members of the same species are also members of the same clone, a group of genetically identical individuals. They are known to attack and even kill anemones from other clones using special nematocysts. Some medusae have primitive eyes. Medusae also have **statocysts,** small, calcareous bodies in fluid-filled chambers surrounded by sensitive hairs. Statocysts give medusae a sense of balance.

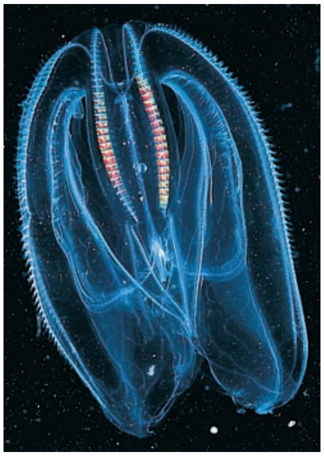


FIGURE 7.12 This comb jelly (*Mnemiopsis leidyi*) displays the rows of ciliary combs characteristic of the group. Four rows are visible here, the middle ones appearing as multicolored bands. The species is common along the Atlantic coast of North America but it has been accidentally introduced into other locations.

COMB JELLIES: RADIAL SYMMETRY REVISITED

The **comb jellies,** or **ctenophores** (phylum **Ctenophora**), are an exclusively marine group of about 100 species. Their radially symmetrical and gelatinous body resembles that of a medusa (Fig. 7.12), but a closer look reveals some unique traits. Ctenophores swim with eight rows of **ciliary combs,** long cilia fused at the base, like combs, that beat in waves. The continuous beating of the ciliary combs refracts light, creating a prism-like, multicolor effect. Body length varies from a few millimeters in the sea gooseberry (*Pleurobrachia*) to 2 m (6.6 ft) in the elongated Venus's girdle (*Cestum;* see Fig. 15.12*c*).

Comb jellies, or ctenophores, are radially symmetrical and similar in appearance to cnidarians but possess eight rows of ciliary combs.

Comb jellies are common in both warm and cold waters. They are carnivores with a voracious appetite. Swarms of comb jellies may consume large numbers of fish larvae and other plankton (see "Biological Invasions: The Uninvited Guests," p. 414). Many capture their prey using two long tentacles armed with sticky cells named **colloblasts.** A few species have nematocysts, possibly obtained by eating jellyfishes or siphonophores.

BILATERALLY SYMMETRICAL WORMS

Radial symmetry works fairly well in animals that attach to surfaces or drift in currents, but animals that crawl or swim in one direction have different needs. Most animals show **bilateral symmetry,** the arrangement of body parts in such a way that there is only one way to cut the body and get two identical halves (Fig. 7.13*b*). Bilaterally symmetrical animals, including humans, have a front, or **anterior,** end and a rear, or **posterior,** end. At the anterior end is a head with a brain, or at least an accumulation of nerve cells, and sensory organs such as eyes. Similarly, bilaterally symmetrical animals have a back, or **dorsal** surface, that is different from the belly, or **ventral** surface. Bilateral symmetry allows animals to be more active in the pursuit of prey and to develop more sophisticated behaviors than those of radially symmetrical animals.

Flatworms

The structurally simplest bilaterally symmetrical body plan is seen in the **flatworms** (phylum **Platyhelminthes**), so called because they are dorsoventrally flattened—that is, they have flat backs and bellies. Flatworms also are the simplest animals in which tissues are organized into real organs and organ systems.

The presence of a **central nervous system** in which information is stored and processed is of special significance. In flatworms it typically consists of a simple **brain,** which is just an aggregation of nerve cells in the head. There are also several nerve cords running from the brain through the length of the worm. The nervous system coordinates the movements of a well-developed muscular system. The gut is similar to those of cnidarians and ctenophores in having only one opening to the outside, the mouth. The space between the outer and inner tissue layers, however, is no longer thin or gelatinous as in cnidarians and ctenophores but is filled with tissue. In developing embryos this middle layer of tissue, the **mesoderm,** gives rise to muscles, the reproductive system, and other organs—not only in flatworms but also in structurally more complex animals. The gut and other internal organs are surrounded by tissue, since there is no body cavity.

Flatworms are bilaterally symmetrical invertebrates typically flattened in appearance. They have true organs and organ systems, including a central nervous system.

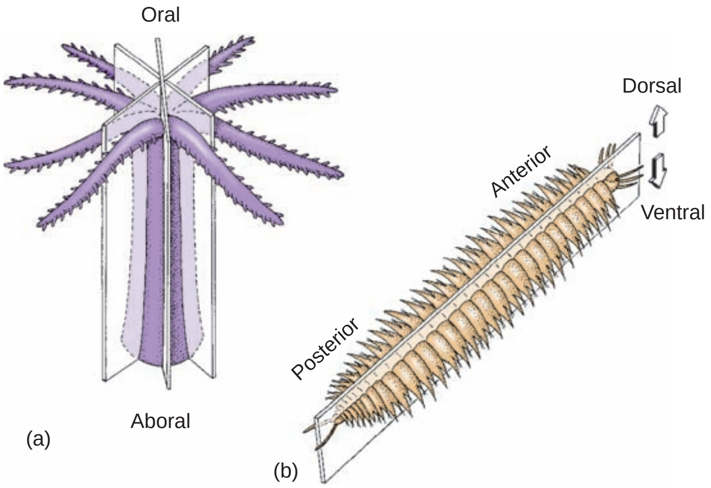


FIGURE 7.13 The radial symmetry of a soft coral's polyp (*a*) in contrast to the bilateral symmetry of a worm (*b*). Bilateral symmetry implies the development of an anterior end with a head, a brain, eyes, and all the other features demanded by more complex behaviors.

There are some 20,000 known species of flatworms. The most commonly seen marine flatworms are the **turbellarians,** a group that consists mostly of free-living carnivores. Most are small, but some are obvious because of their striking color patterns (Fig. 7.14). Some turbellarians live inside or on the surface of oysters, crabs, and other invertebrates.

Flukes, or **trematodes,** are the largest group of flatworms, with more than 6,000 species. All flukes are **parasites,** which live in close association with other animals and feed on their tissues, blood, or intestinal contents. Like most parasites, flukes have complex life histories with amazing reproductive abilities, a key to their success. Adult flukes always live in a vertebrate. The larvae may inhabit invertebrates like snails or clams or vertebrates like fish. The larva must then be eaten by the vertebrate destined to harbor the adult. Flukes are common in fishes, seabirds, and whales.

Tapeworms, or **cestodes,** are parasitic flatworms that, with a few exceptions, have a long body consisting of repeated units. These unique worms live inside the intestine of most species of vertebrates, including marine ones. The head of the worm attaches to the walls of the gut by suckers, hooks, or other structures. Tapeworms lack a gut or mouth. They absorb nutrients from their host's intestinal contents directly across the body wall. Their larvae are found in invertebrates or vertebrates. Tapeworms may reach a prodigious length. The record appears to be a species found in sperm whales that is 15 m (50 ft) long!

Ribbon Worms

Though they look like long flatworms, **ribbon,** or **nemertean, worms** (phylum **Nemertea**) show several features that indicate a more complex degree of organization. Their digestive tract is complete, with a gut that includes a mouth and an anus to get rid of undigested material. They also have a **circulatory system,** by which blood transports nutrients and oxygen to tissues. The most distinctive feature of ribbon worms, however, is their **proboscis**

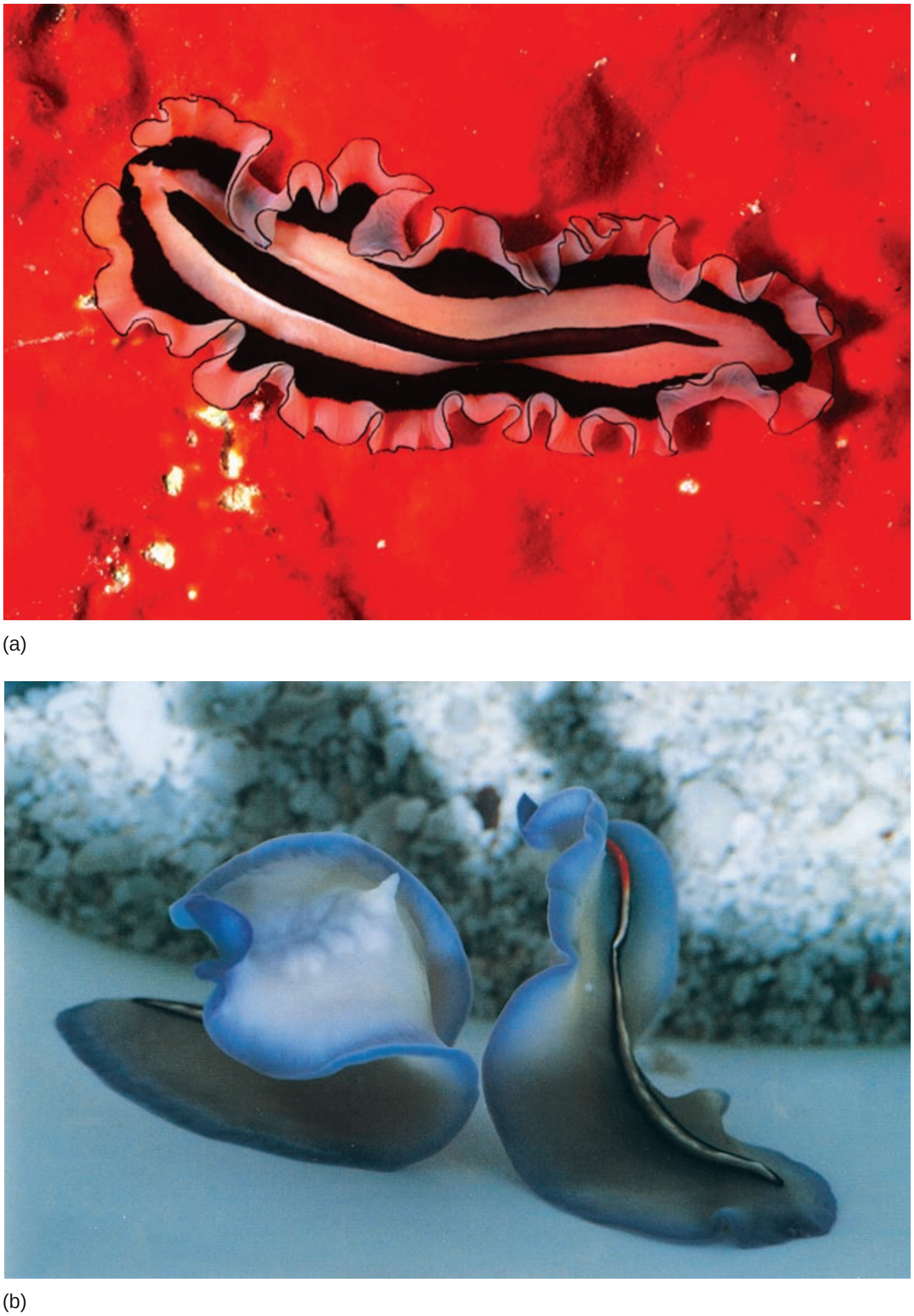


FIGURE 7.14 (*a*) A turbellarian flatworm (*Pseudobiceros gratus*) from Australia's Great Barrier Reef. (*b*) Turbellarian flatworms (*Pseudoceros bifurcus*) joust in a mating ritual known as penis fencing. The worms are hermaphrodites, and each tries to penetrate the skin of the other with its needle-like penis to inject its sperm. The first to succeed acts as the male and avoids the energy costs of healing the wound and developing eggs.

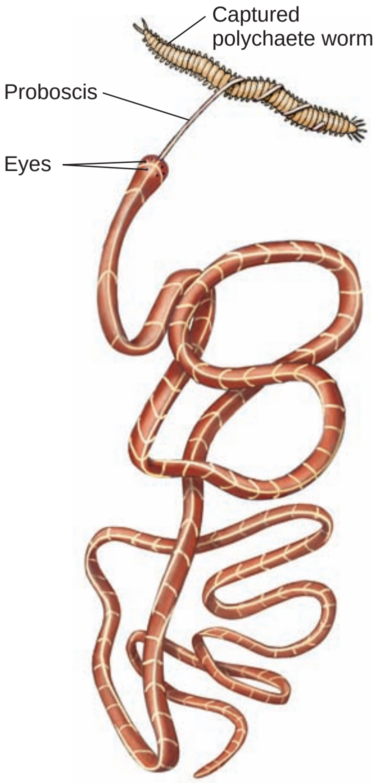


FIGURE 7.15 Ribbon, or nemertean, worms use a proboscis to entangle prey. The proboscis secretes toxins and may be armed at the tip with a spine. Once the prey is captured, the proboscis is pulled back and it's dinnertime.

(Fig. 7.15), a long, fleshy tube used to entangle prey. It is everted from a cavity above the mouth like the finger of a glove. All ribbon worms are predators that feed on worms and crustaceans.

There are approximately 900 species of ribbon worms, most of which are marine. They are found in all oceans but are most common in shallow temperate waters. Some are nocturnal and not easily seen; others are brightly colored and may be found under rocks at low tide. Ribbon worms are incredibly elastic, and the proboscis may extend a meter or more beyond the body. One species reaches 30 m (100 ft) long, which makes it the longest invertebrate on earth.

Nematodes

Nematodes (phylum **Nematoda**), some of which are known as **roundworms,** are hardly ever seen, but their numbers in sediments, particularly those rich in organic matter, can be staggering. Many species are parasitic, and most groups of marine organisms have nematode parasites. Nematodes are perfectly adapted to live in sediments or the tissues of other organisms. They are mostly small, with slender and cylindrical bodies that are typically pointed at both ends (see the figure in "Life in Mud and Sand," p. 291). Nematodes that inhabit sediments feed mostly on bacteria and organic matter. The gut, which ends in an anus, lies within a **body cavity** filled with fluid that transports nutrients. A layer of muscles in the tough but flexible body wall pushes and squeezes against the fluid, which acts as a **hydrostatic skeleton** that provides support and aids in locomotion.

Nematodes are very common inhabitants of marine sediments and are widespread parasites of most groups of marine animals.

The actual number of species of nematodes is debatable. Estimates vary between 10,000 and 25,000 species, but some biologists believe there may be as many as half a million remaining to be discovered.

The adults of *Anisakis* and a few related nematodes inhabit the intestine of seals and dolphins. Their larvae, however, are found in the flesh of many types of fish and may infect humans who eat raw or poorly cooked fish. Often the larvae are vomited or coughed up without further complications. Sometimes, however, larvae penetrate into the walls of the stomach or intestine, causing symptoms similar to those of ulcers. It is a risk that lovers of raw fish dishes such as *sashimi* and *ceviche* must take.

Segmented Worms

A large group of perhaps as many as 20,000 species, the **segmented worms,** or **annelids** (phylum **Annelida**), includes earthworms and many marine worms. Their body plan includes innovations that have been incorporated in some of the more structurally complex groups of animals. The body consists of a series of similar compartments, or **segments,** a condition known as **segmentation.** Segmentation can be clearly seen in the rings of the familiar earthworm. The gut goes through all the segments and lies in a cavity known as a **coelom** (Fig. 7.16*c*). The coelom is entirely surrounded by a different type of tissue, which develops from mesoderm in contrast to the simpler body cavity of nematodes. It is present in all of the remaining structurally complex phyla. The coelom of segmented worms is filled with fluid and divided by partitions that correspond to the external segments. The segments act as a hydrostatic skeleton and can be contracted in sequence by means of muscles in the body wall. **Longitudinal muscles** (Fig. 7.16*c*) lengthen and shorten the segments, whereas **circular muscles** increase or reduce their diameter. These movements, plus the flexibility given by segmentation, make annelids efficient crawlers and burrowers.

Polychaetes Almost all marine annelids are **polychaetes** (class **Polychaeta**), which are common and important in many environments. Each of the body segments of most polychaetes has a pair of flattened extensions, or **parapodia,** which are provided with stiff and sometimes sharp bristles, or **setae** (Fig. 7.16).

Annelids have a body consisting of similar segments and a coelom. Most marine annelids are polychaetes, segmented worms that have parapodia.

Like all annelids, polychaetes have a circulatory system that transports nutrients, oxygen, and carbon dioxide. Circulating blood always remains within distinct blood vessels (Fig. 7.16*c*), making it a **closed circulatory system.** Muscular contraction of vessels helps in the circulation of blood. Wastes from the coelom are removed by a pair of **excretory organs** in each segment (Fig. 7.16*c*).

In small animals, oxygen—essential in the release of energy through **respiration**—can easily move from the water across the body wall to all the tissues. In the larger and relatively more active polychaetes, however, obtaining enough oxygen from the water is

Respiration

organic matter + $O_2 \rightarrow CO_2 + H_2O$ + energy
(glucose)

- Chapter 4, p. 67

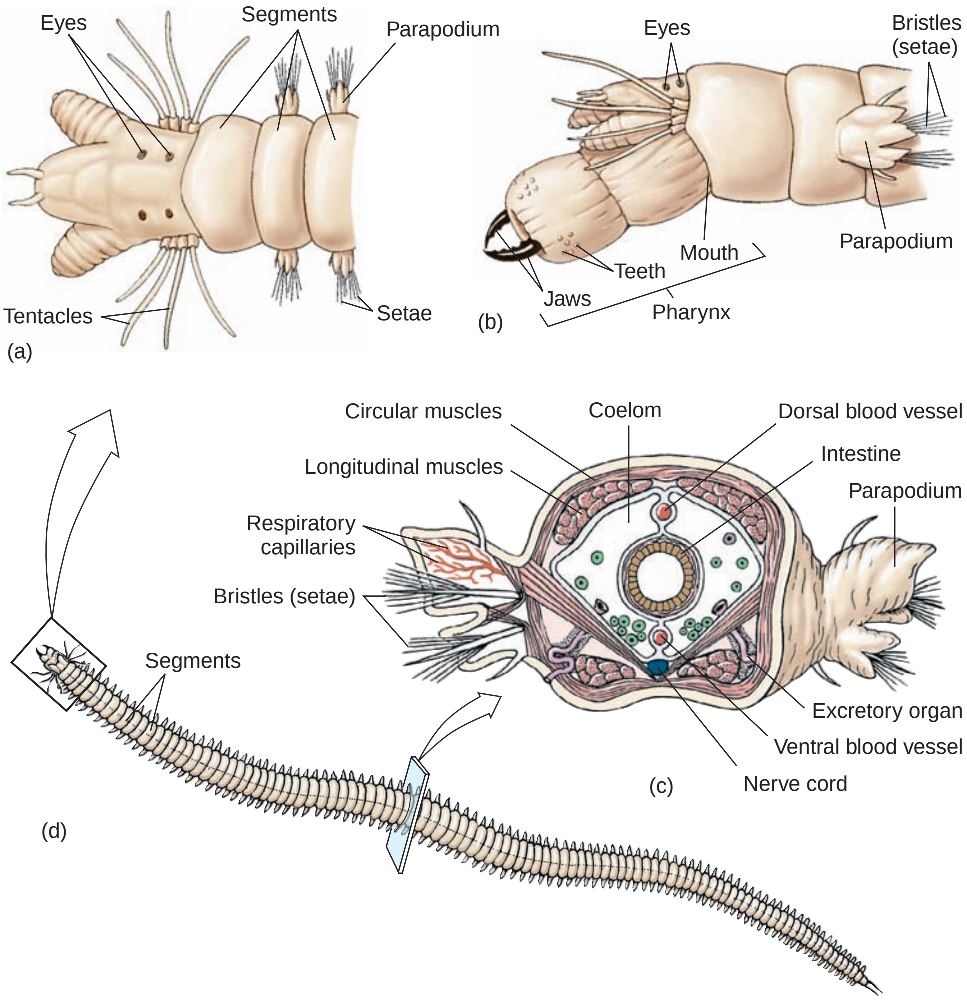


FIGURE 7.16 This sandworm (*Nereis*) illustrates the meaning of the name polychaetes—"many setae, or bristles." (*a*) Dorsal view of the head, with the pharynx retracted, showing the sensory tentacles and eyes. (*b*) Side view of the head, showing the large pharynx in an extended position. (*c*) Section across a segment. (*d*) Dorsal view of the worm.

a potential problem. Polychaetes have solved this problem by evolving **gills** on the parapodia or elsewhere (Fig. 7.16*a*). The gills are thin-walled extensions of the body wall that have many blood vessels called **capillaries,** which allow for the easy absorption of oxygen. Capillaries may also be found on the walls of the parapodia (Fig. 7.16*c*). This absorption of oxygen, along with the elimination of carbon dioxide, is known as **gas,** or **respiratory, exchange.**

The life history of many polychaetes involves a planktonic larval stage known as the **trochophore,** which has a band of cilia around the body (see Fig. 15.11*d*). The trochophore is of considerable interest because it is also one of the larval stages in some other groups of invertebrates. The types of larvae, among other characters, are used by biologists to deduce evolutionary relationships among different groups of invertebrates.

The more than 10,000 species of polychaetes are almost entirely marine. Length varies a great deal but is typically 5 to 10 cm (2 to 4 in). Many polychaetes crawl on the bottom, hiding under rocks or coral. These crawling worms, such as most sandworms (*Nereis*), are mostly carnivores. They feature heads provided with several pairs of eyes and other sense organs (see Fig. 7.16) used to search for small invertebrates. A proboscis, often armed with jaws, is used to capture prey. The parapodia are well developed and are used in locomotion.

Other polychaetes burrow in mud or sand (see Fig. 11.31). Many, like bloodworms (*Glycera*), capture small prey. Others, like lugworms (*Arenicola*), are deposit feeders (see Fig. 7.3).

Many polychaetes live in temporary or permanent tubes, either singly or in aggregations (see Figs. 12.11 and 13.6). The tubes may be made of mucus, protein, bits of seaweed, cemented mud particles, sand grains, or tiny fragments of shells. Tube-dwelling polychaetes usually have reduced parapodia. Some, such as *Terebella* and related forms (see Fig. 13.11), are suspension feeders. Their tentacles have cilia and mucus that catch organic particles in the water and move them to the mouth (see Fig. 7.3). Fanworms, or featherduster worms (*Sabella;* Fig. 7.17*b*), use feathery tentacles covered with cilia to capture, sort, and transport particles. Serpulids (*Serpula*) and spirorbids (*Spirorbis*), also suspension feeders, extend featherlike tentacles from calcium carbonate tubes they build on rocks and other surfaces (see Fig. 13.17).

Polychaetes are also successful at other lifestyles. Species of *Tomopteris* are planktonic throughout life. Their parapodia are flat and expanded to help in swimming (see Fig. 15.12*d*). In the tropical Pacific the bodies of the Palolo worm (*Eunice*) periodically break off, and the posterior half swims up to the surface to spawn. This behavior, known as **swarming,** is timed in some areas with the phases of the moon, reaching its peak just after full moon. This bit of information is useful because in some places people gather the worms for food.

Some polychaetes live on the external surface of such invertebrates as sea stars and sea urchins. Several species live in the burrows of other invertebrates or inhabit shells occupied by hermit crabs.

Beard worms, or **pogonophorans,** are highly specialized annelids. They lack a mouth and gut. Except for sponges and tapeworms, this phenomenon is uncommon in animals. A tuft of one to many thousand long tentacles (Fig. 7.18), responsible for the group's common name, appears to be involved in absorbing nutrients

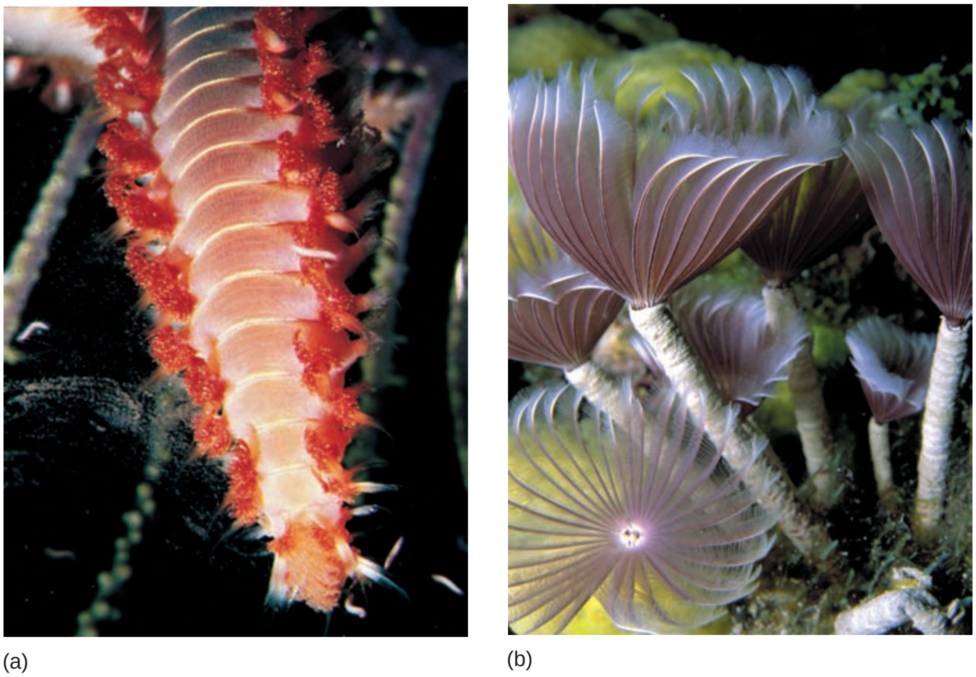

(a) (b)

FIGURE 7.17 Polychaetes are common inhabitants of most marine bottoms. (*a*) The anterior end of a free-living polychaete (*Hermodice carunculata*), a fireworm that feeds on corals. The bright red structures are gills. (*b*) *Sabella melanostigma*, a feather-duster worm, inhabits leathery tubes.

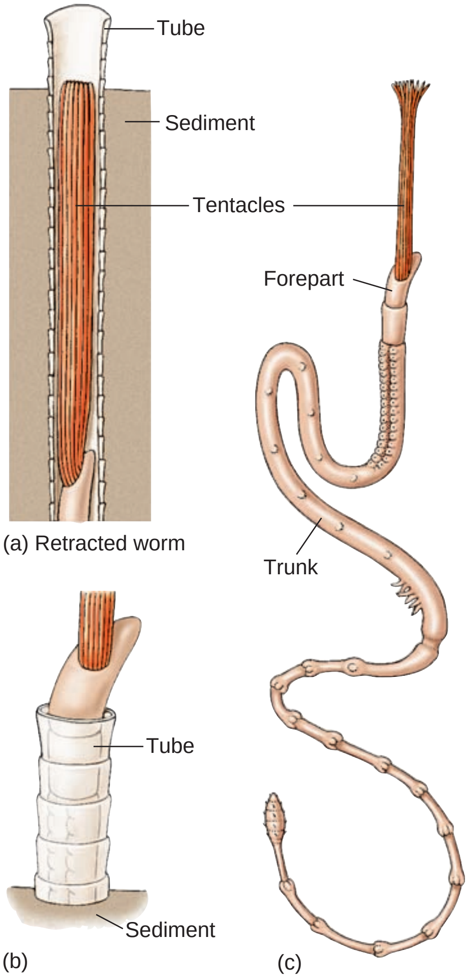


FIGURE 7.18 Diagrammatic representation of a beard worm, or pogonophoran. (*a*) Most secrete and live in tubes buried in the soft sediment. (*b*) Only the upper end of the tube protrudes, with the tentacle or tentacles extending from it. (*c*) Worm removed from its tube.

dissolved in the water. Some beard worms have **symbiotic** bacteria that use the nutrients to manufacture food, which in turn is used by the worms.

Approximately 135 species of beard worms are known. They are mostly restricted to deep water, which helps explain why they remained unknown until 1900. Beard worms were once grouped as a separate phylum (see "How to Discover a New Phylum," p. 128). The total length of the worms ranges from 10 cm to 2 m (4 in. to 7 ft). A group related to beard worms, the **vestimentiferans,** are even longer. Large numbers of these worms have been found at hydrothermal vents (see Figs. 16.28 and 16.29).

Oligochaetes **Oligochaetes** are small worms found in mud and sand (see "Life in Mud and Sand," p. 291), where they feed on detritus. They are the marine relatives of earthworms. Some species may be very abundant. Unlike most polychaetes, oligochaetes lack parapodia.

Leeches Bloodsucking **leeches** (class **Hirudinea**) live mostly in fresh water, but marine species can be found attached to marine fishes and invertebrates. Leeches are highly specialized annelids distinguished by a sucker at each end and no parapodia.

Peanut Worms

Often called **peanut worms,** the **sipunculans** (phylum **Sipuncula**) have soft, unsegmented bodies with a coelom. They burrow in muddy bottoms, rocks, and corals or hide in empty shells. All are marine, living mostly in shallow water. The long anterior portion contains a mouth and a set of small lobes or branching tentacles (Fig. 7.19). These can be pulled into the remaining portion of the body, and the worm then becomes a compact bundle that looks like a large peanut. Peanut worms are 1 to 35 cm (0.4 to 14 in) long. Approximately 320 species are known, all deposit feeders.

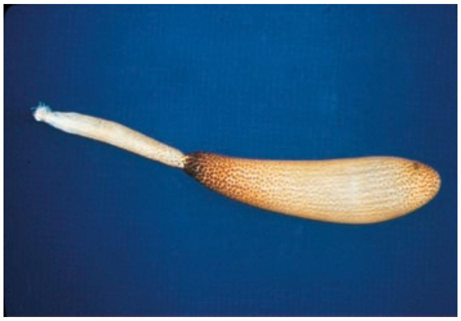


FIGURE 7.19 *Antillesoma antillarum*, a peanut worm (or sipunculan), burrows in coral and rocks in the Caribbean. The anterior portion, which is extended in this specimen, can be retracted.

Echiurans

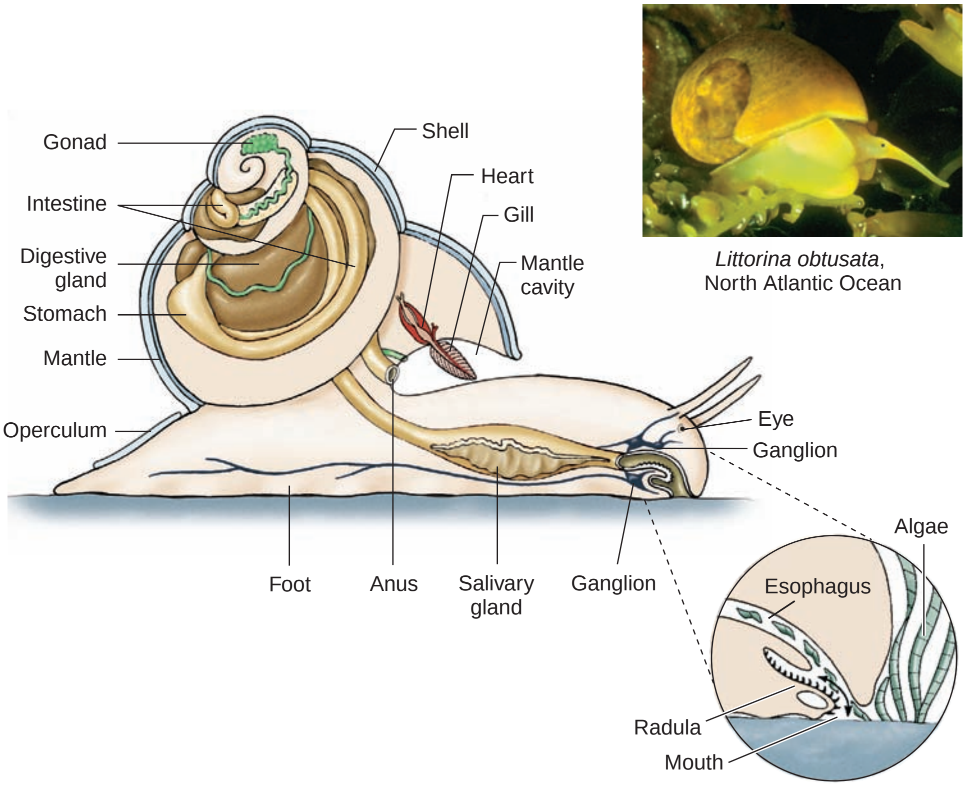
All of the 135 known species of **echiurans** (phylum **Echiura**) are marine. They look like soft, unsegmented sausages buried in the mud or in coral. They are similar to peanut worms in shape and size except for having a non-retractable, spoon-like or forked proboscis (see Fig. 13.9). Some biologists consider them to be annelids. Echiurans are deposit feeders that use the proboscis to gather organic matter. The "fat innkeeper" (*Urechis caupo*) of the western coast of North America lives in **U**-shaped tubes in mud (see Fig. 12.11).

MOLLUSCS: THE SUCCESSFUL SOFT BODY

Snails, clams, octopuses, and other familiar forms are members of the phylum **Mollusca. Molluscs** have been very successful: there are more species of molluscs in the ocean than of any other animal group. There may be as many as 200,000 species of molluscs, which are surpassed only by the arthropods as the largest phylum of animals.

Most molluscs have a soft body enclosed in a calcium carbonate shell (Fig. 7.20). The body is covered by a **mantle,** a

Symbiosis The living together in close association of two different species.
- Chapter 10, p. 218



Littorina obtusata, North Atlantic Ocean

FIGURE 7.20 The general body plan of a gastropod, indicating the most important internal structures. In many species the head and foot can be retracted into the shell, leaving a tough operculum blocking the shell opening.

How to Discover a New Phylum

It is not very difficult to discover a new marine invertebrate species. Small animals living in sediments, among rocky shore seaweeds, in crevices or holes in coral, or in deep water are good candidates. Discovering a new phylum of invertebrates, however, is a different story.

The founding species of three phyla escaped description until relatively recently. All three are exclusively marine.

The first species of what eventually became the new phylum **Gnathostomulida** was not officially described until 1956. Gnathostomulids are a group of about 100 species of minute worms living among sediment particles around the world (see the figure in "Life in Mud and Sand," p. 291). They are similar to the flatworms but possess unique features, including a set of toothed jaws to scrape bacteria, diatoms, and other organisms from sand grains.

The next of the new phyla has a short but turbulent history. In 1961 Robert Higgins, then at the Smithsonian Institution in Washington, D.C., predicted the existence of a group that lived in the spaces between clean, coarse sediment particles in deep water. He actually found a specimen in 1974 but, unfortunately, did not realize it was something new.

One year later, in 1975, Reinhardt Kristensen of the University of Copenhagen, Denmark, collected a specimen, but it was destroyed while being prepared for microscopic examination. Kristensen later found larvae of the elusive animal in coarse sediments from western Greenland and the Coral Sea. In 1982 he was working with a large sample off the coast of Brittany in France. It was his last day at the Roscoff Biological Station, and to save time he washed the sample with fresh water instead of following the standard but more time-consuming method. It happened to loosen the grip of the animals on the sediment particles, and Kristensen got a complete series of larval and adult specimens.

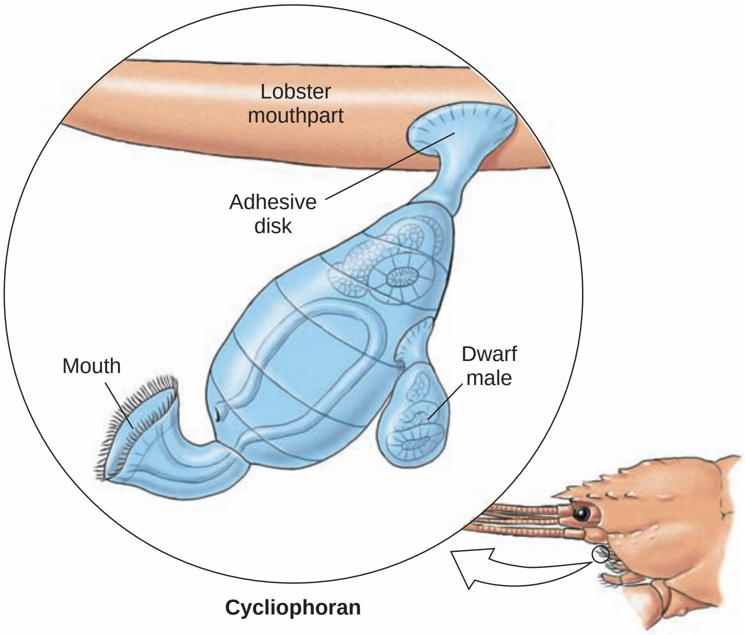
The microscopic animals Kristensen found have a body encased by six plates. The head, which can be retracted, bears a set of spines and a mouth at the end of a cone. Kristensen got together with Higgins, and they concluded that the specimens Higgins examined in 1974 and those subsequently found by Kristensen were members of a new phylum. They found additional adults in eastern Florida, which further confirmed the new status of the group.

The new phylum **Loricifera** (meaning "armor bearer") was officially born in 1983 when Kristensen published a paper in a German scientific journal. The first species was named *Nanaloricus mysticus* ("mystic, or enigmatic, dwarf armor"), and the larva was baptized the Higgins larva in honor of Higgins—a nice consolation prize, indeed! Some 20 additional species have so far been described. About 100 new species have been collected but not yet officially described.

The latest new phylum comes from another unexpected location: the hairs around a Norway lobster's mouth. Though first observed in the 1960s, the phylum **Cycliophora** was not described until 1995. So far it consists of one species, *Symbion pandora*, a tiny, bottle-shaped sac with a disk-like mouth. Cilia around the mouth sweep food particles that come off the lobster's mouth at mealtime.

This strange lifestyle coincides with a bizarre life cycle. The minute but multicellular animal—hundreds often live on a lobster—alternates sexual and asexual generations. Dwarf males, which live attached to females, exist only to produce sperm. Females also reproduce asexually, but they produce only females that develop inside box-like structures inside their mothers. The new generation of females is set free from the boxes as it bursts out from the mothers. The Greek myth of a box that Pandora (and hence the name of the first cycliophoran) opened to allow all human ills to escape is thus re-created around a lobster's mouth.

A second species of *Symbion* was described from the American lobster. A third species, not yet described, has been discovered on the European lobster.



Cycliophoran

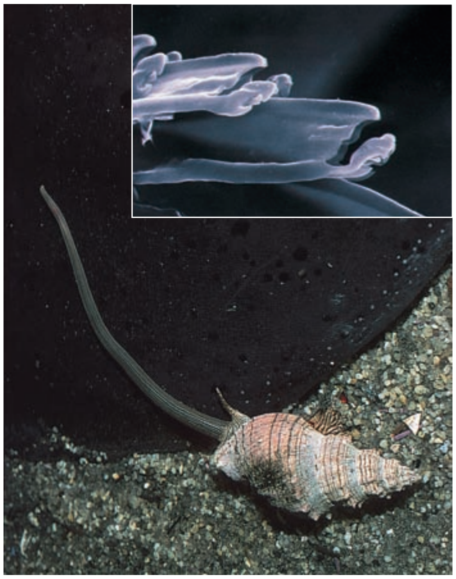


FIGURE 7.21 The Cooper's nutmeg snail (*Cancellaria cooperi*) seeks out electric rays, which rest partially buried in sand. It then extends its long proboscis, makes a tiny cut in the ray's skin with the radula at the end of the proboscis, and then sucks the ray's blood. A high-magnification photo (inset) shows the teeth of the radula.

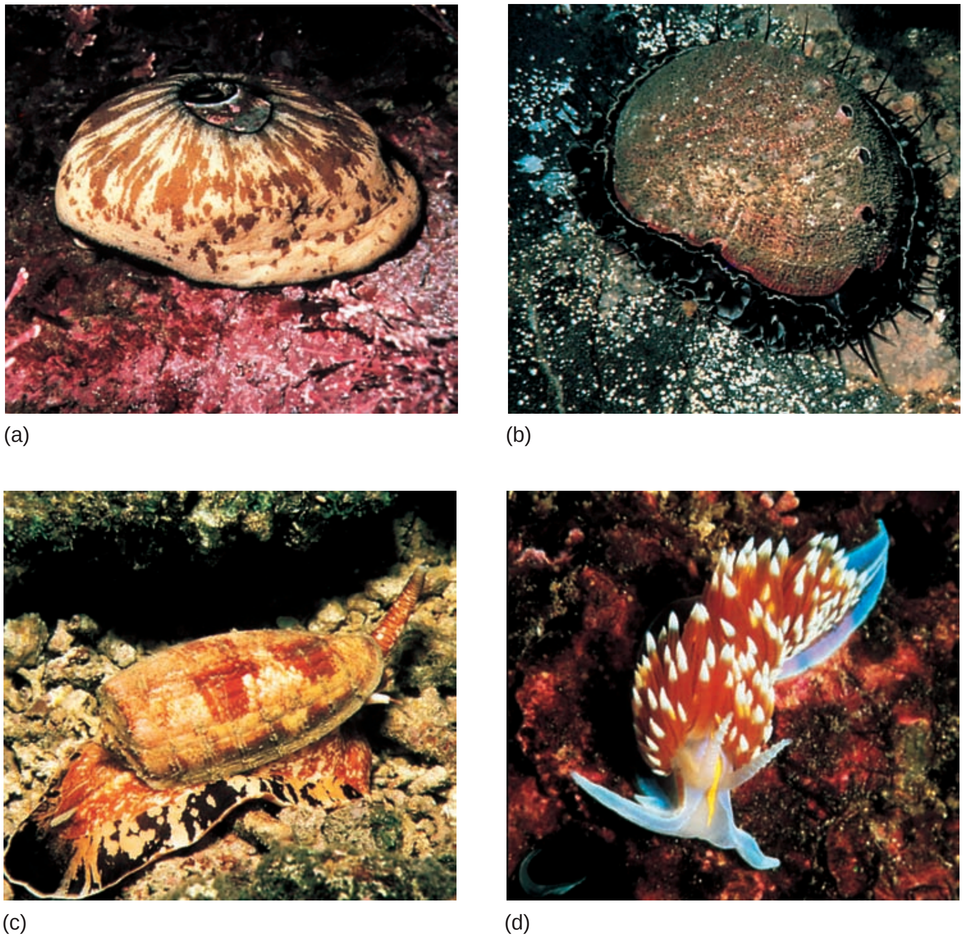


FIGURE 7.22 Gastropods come in all shapes, colors, and habits. (*a*) The giant keyhole limpet (*Megathura crenulata*), from the Pacific coast of North America, photographed on a bottom covered by encrusting red coralline algae. (*b*) The red abalone (*Haliotis rufescens*) is much sought after for food and is now rare in some areas. (*c*) Cone shells, such as *Conus geographus*, are carnivorous snails that bury themselves in sand, waiting for prey such as small fishes. Their radula is modified into a dart-like tooth that is shot—together with a poison—into the unsuspecting prey, which is eaten whole, very much as in snakes (also see Fig. 10.7). (*d*) A flashy nudibranch (*Phidiana crassicornis*).

thin layer of tissue that secretes the shell. The unsegmented body is typically bilaterally symmetrical. There is a ventral, muscular **foot,** usually used in locomotion. Most molluscs have a head that normally includes eyes and other sensory organs. A feature unique to molluscs is the **radula,** a ribbon of small teeth that is used to feed, usually by rasping food from surfaces (Fig. 7.20). The radula is modified in carnivorous molluscs (Figs. 7.21 and 10.7). The radula is made largely of **chitin,** a highly resistant carbohydrate also found in other invertebrates. Gas exchange is through paired gills. The body cavity, a coelom, is much reduced, being restricted to small cavities around the heart and a few other organs.

All molluscs have this basic body plan, but it is often greatly modified. The shell, for example, is internal in squids and absent in octopuses and a few other groups. In snails portions of the body are coiled and asymmetrical. In some molluscs the radula is modified or even absent.

The molluscs constitute the largest group of marine animals. Their body is soft with a muscular foot. They usually have a shell and a radula, a rasping "tongue" unique to the group.

Types of Molluscs

Molluscs exhibit an immense diversity of structure and habit. They occupy all marine environments from the wave-splashed zone of rocky shores to hydrothermal vents in the deep sea. They thrive on practically every conceivable type of diet. For all their diversity, though, most molluscs belong to one of three major groups.

Gastropods The **gastropods** (class **Gastropoda**), are the largest, most common, and most varied group of molluscs. Snails are the most familiar gastropods, but the group includes other forms such as limpets, abalones, and nudibranchs (Fig. 7.22). There are perhaps 75,000 species, mostly marine. A typical gastropod can best be described as a coiled mass of vital organs enclosed by a dorsal shell (see Fig. 7.20). The shell rests on a ventral creeping foot (the term "gastropod" means "stomach footed") and is usually coiled.

Most gastropods use their radula to scrape algae from rocks, as in periwinkles (*Littorina;* see Fig. 11.2), limpets (*Fissurella, Lottia;* Fig. 7.22*a*), and abalones (*Haliotis;* Fig. 7.22*b*). Some, like mud snails (*Hydrobia*), are deposit feeders on soft bottoms. Whelks (*Nucella, Buccinum;* see Fig. 11.21), oyster drills (*Murex, Urosalpinx*), and cone shells (*Conus;* Fig. 7.22*c*), are carnivores. They prey on clams, oysters, worms, and even small fishes. The violet snail *Janthina* has a thin shell and produces a bubble raft out of mucus to float on the surface, looking for siphonophores, its prey (see Fig. 15.15). Sea hares (*Aplysia*), whose shells are small, thin, and buried in tissue, graze on seaweeds.

Nudibranchs, or **sea slugs,** are gastropods that have lost the shell altogether. Colorful branches of the gut or exposed gills make nudibranchs among the most beautiful of all marine animals (Fig. 7.22*d*). They prey on sponges, hydroids, and other invertebrates. As a defensive mechanism, nudibranchs often produce noxious chemicals or retain undischarged nematocysts taken undigested from their prey.

Bivalves Bivalves (class **Bivalvia**) are clams, mussels, oysters, and similar molluscs. In bivalves the body is laterally compressed (that is, flattened sideways) and enclosed in a shell with two parts, or **valves** (Fig. 7.23). The **umbo**, the upper hump near the hinge of each shell, is the oldest part of the shell. Growth from the umbo proceeds in the form of concentric growth lines. There is no head to speak of, and no radula. The gills, expanded and folded, are used not only to obtain oxygen but also to filter and sort small food particles from the water. The inner surface of the shell is lined by the mantle, so that the whole body lies in the **mantle cavity,** a large space between the two halves of the mantle. Strong muscles, the **adductor muscles,** are used to close the valves.

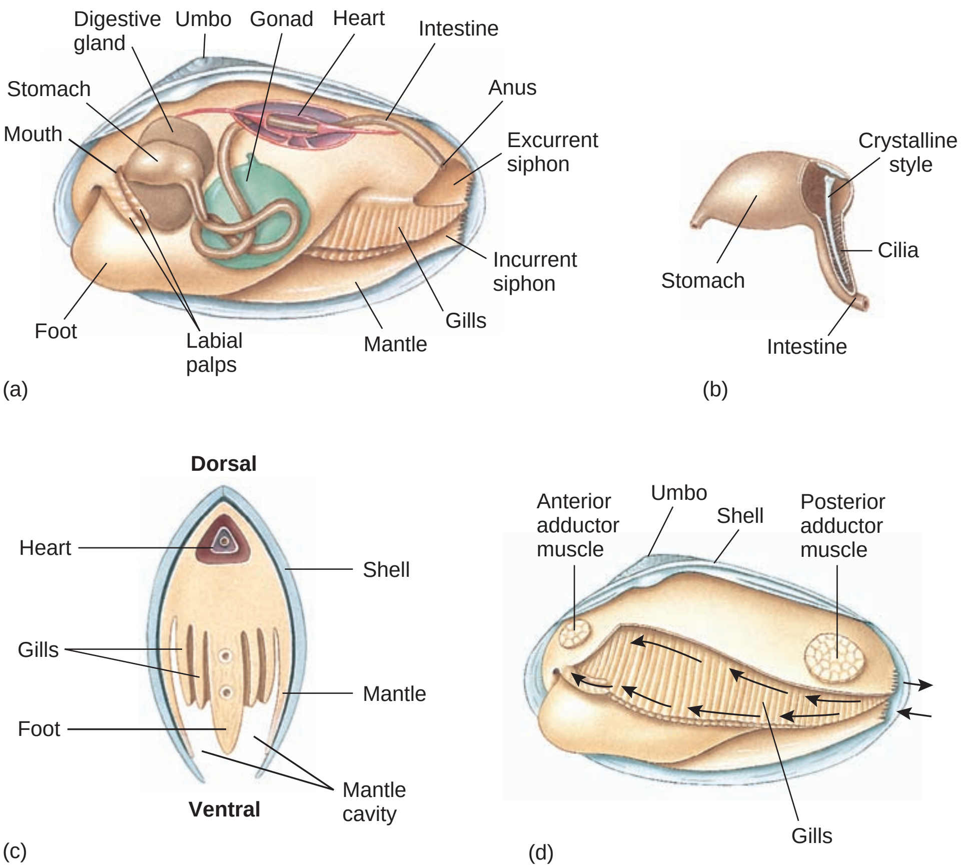


FIGURE 7.23 A laterally compressed body is the most distinctive feature of bivalves, illustrated here by a clam. The gills, which hang on both sides of the body (*a*, *c*), sort out food particles and transport them to the mouth with the help of cilia and mucus. The palps then push the food into the mouth. Food is digested in the stomach with the help of the crystalline style (*b*). The path of the particles from the incurrent siphon to the mouth is indicated by arrows (*d*).

Clams (*Macoma, Mercenaria*) use their shovel-shaped foot to burrow in sand or mud (see Figs. 11.30 and 12.11). When the clam is buried, water is drawn in and out of the mantle cavity through **siphons** formed by the fusion of the edge of the mantle (Fig. 7.23*a* and *d*). This allows clams to feed and obtain oxygen while buried in sediment.

Not all bivalves are burrowers. Mussels (*Mytilus;* see Fig. 11.4), for instance, secrete strong **byssal threads** that attach them to rocks and other surfaces. Oysters (*Ostraea, Crassostrea;* Fig. 7.24*a*) cement their left shell to a hard surface, often the shell of another oyster. Aphrodisiac or not, they have been lustfully swallowed by lovers of good food for thousands of years. Pearl oysters (*Pinctada*) are the source of most commercially valuable pearls. Pearls are formed when the oyster secretes shiny layers of calcium carbonate to coat irritating particles or parasites lodged between the mantle and the iridescent inner surface of the shell, which is called mother-of-pearl. Cultured pearls are obtained by carefully inserting a tiny bit of shell or plastic into the mantle. Some scallops (*Pecten, Lima;* Fig. 7.24*b*) live unattached and can swim for short distances by rapidly ejecting water from the mantle cavity and clapping the valves. The largest bivalve is the giant clam (*Tridacna;* see Fig. 14.34), which grows to more than 1 m (3 ft) in length.

Many bivalves bore in coral, rock, or wood. The shipworm (*Teredo*) bores in mangrove roots, driftwood, and wooden structures such as boats and pilings. They use their small valves to excavate the wood, which is eaten. Symbiotic bacteria in the shipworm's gut digest the wood. The rasping valves lie at the inner end of a tunnel lined with calcium carbonate, and a tiny siphon protrudes from the entrance at the other end. Shipworms are an example of a **fouling organism,** one that settles on the bottoms of boats, pilings, and other submerged structures.

Cephalopods The **cephalopods** (class **Cephalopoda**), predators that are specialized for locomotion, include the octopuses, squids, cuttlefishes, and other fascinating creatures. Cephalopods adapt the molluscan body plan to an active way of life. Nearly all are agile swimmers with a complex nervous system and a reduction or loss of the shell. All 650 living species are marine. A cephalopod (the name means "head-footed") is like a gastropod with its head pushed down toward the foot. The foot is modified into arms and tentacles, usually equipped with suckers that are used

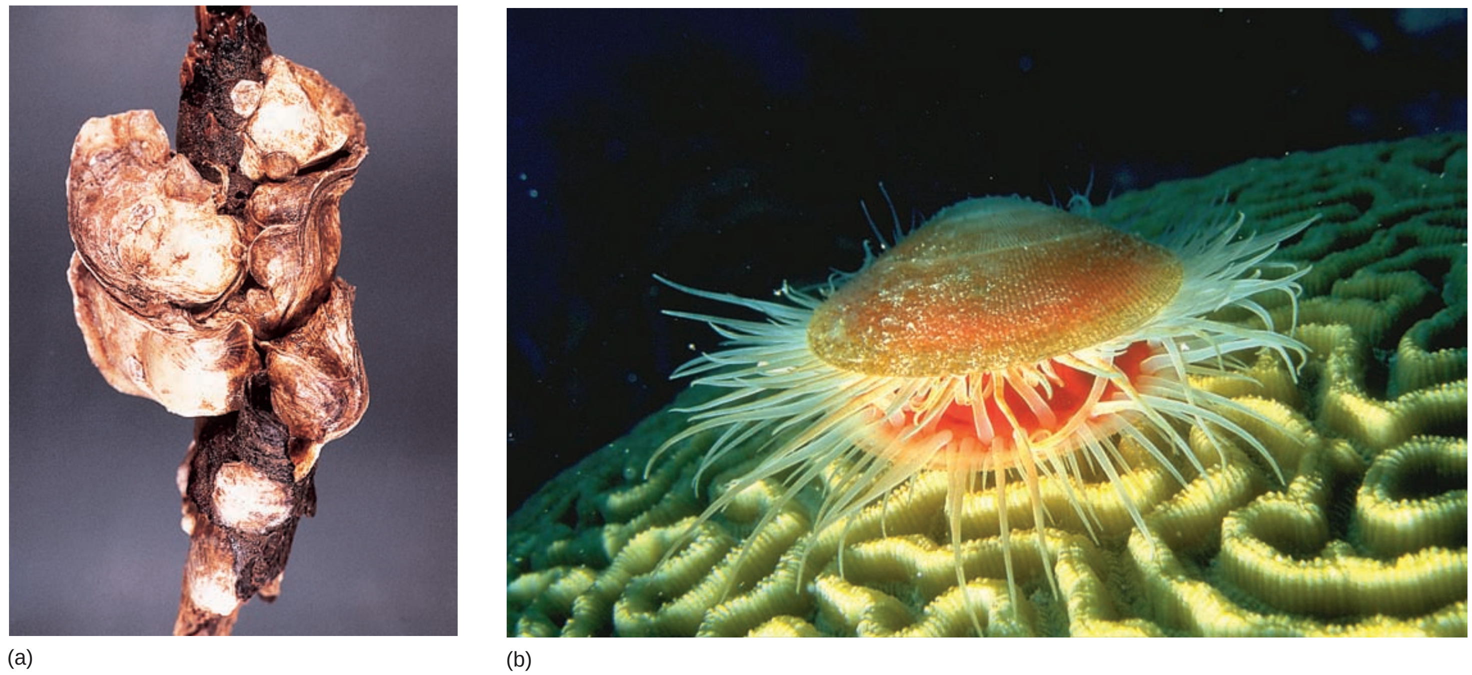
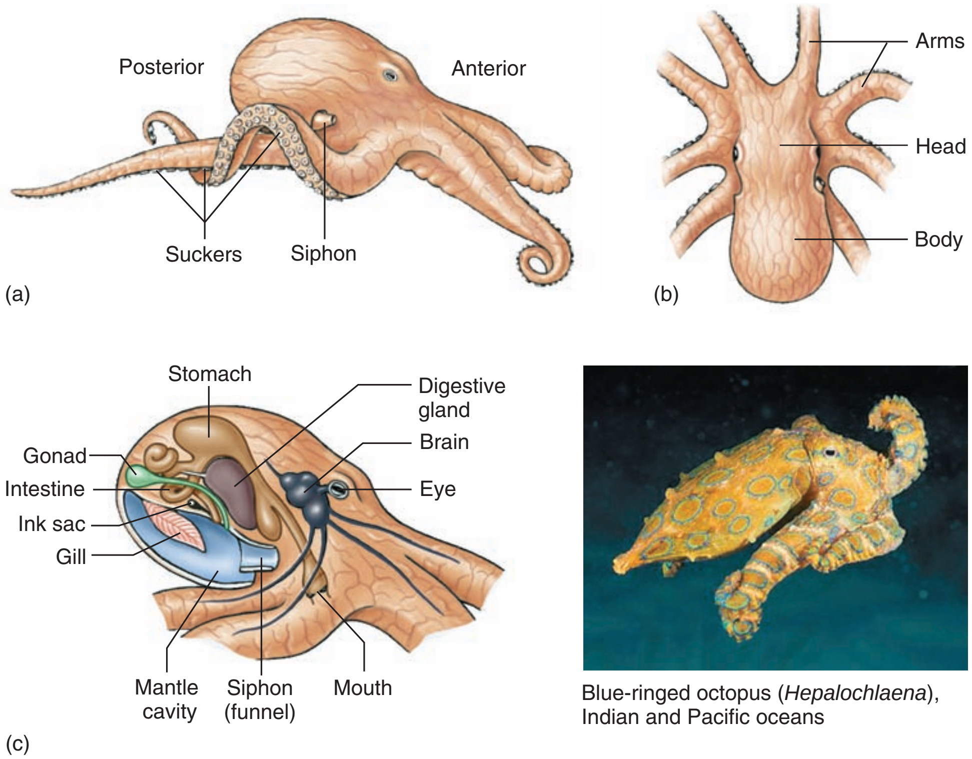


FIGURE 7.24 Oysters such as *Crassostrea virginica* (*a*) are harvested commercially around the world (see Fig. 17.15). Some bivalves, like scallops and the file clam (*Lima scabra, b*) live free on the bottom. Others bury themselves in sand or mud.



Blue-ringed octopus (*Hepalochlaena*), Indian and Pacific oceans

FIGURE 7.25 External (*a* and *b*) and internal (*c*) structure of the octopus. In the male the tip of the third right arm is modified to transfer packets of sperm from his siphon into the mantle cavity of the female. Copulation is preceded by courtship behavior that includes intricate color changes.

to capture prey (Fig. 7.25) The large eyes, usually set on the sides of the head, are remarkably like ours. The body, rounded in octopuses and elongated in squids, is protected by a thick and muscular mantle. The mantle forms a mantle cavity behind the head that encloses two or four gills. Water enters through the free edge of the mantle and leaves through the **siphon,** or **funnel,** a muscular tube formed by what remains of the foot, which projects under the head. Cephalopods swim by forcing water out of the mantle cavity through the siphon. The flexible siphon can be moved around, allowing the animal to move in practically any direction, an example of jet propulsion in nature.

Octopuses (*Octopus*)—not "octopi"—have eight long arms and lack a shell (Fig. 7.25). They are common bottom dwellers. Including arms, the size varies from 5 cm (2 in) in the dwarf octopus (*Octopus joubini*) to a record of 9 m (30 ft) in the Pacific giant octopus (Fig. 7.26*a*).

Octopuses are efficient hunters, with crabs, lobsters, and shrimps among their favorite dishes. They bite their prey with a pair of beak-like jaws. The radula may help rasp away flesh. They also secrete a paralyzing substance, and some have a highly toxic bite. Most, however, are harmless. They use crevices in rocks, and even discarded bottles and cans, as homes. Their shelters are given away by the presence of rocks, which they move around, and by the remains of crabs. Like most other cephalopods, they can distract potential predators by emitting a cloud of dark fluid produced by the **ink sac** (Fig. 7.27).

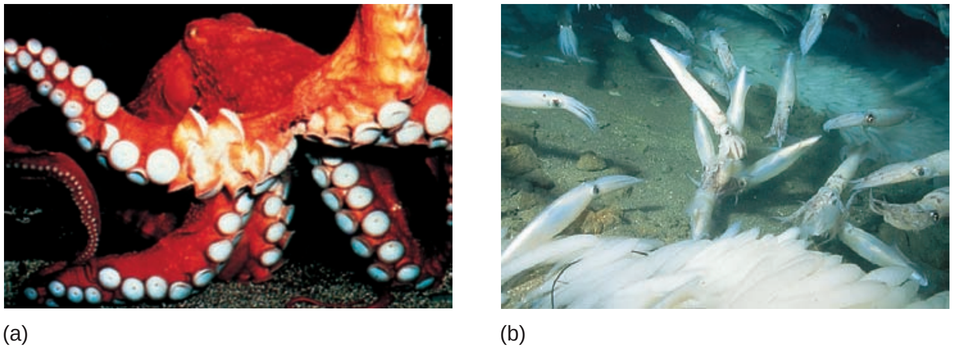

(a) (b)

FIGURE 7.26 (*a*) The Pacific giant octopus (*Enteroctopus dofleini*). (*b*) Mating squids (*Loligo opalescens*). Notice the masses of white, gelatinous egg cases on the bottom.

Squids (*Loligo;* Figs. 7.26*b* and 7.27) are better adapted for swimming than are octopuses. The body is covered by the mantle, which has two triangular fins (Fig. 7.27). The arrangement of the internal organs is similar to that of the octopus (see Fig. 7.25*c*), except that the squid's body is elongated. Squids can remain motionless in one place or move backward or forward just by changing the direction of the siphon. Eight arms and two tentacles, all with suckers, circle the mouth. The tentacles are long and retractable and have suckers only at the broadened tips. They can be swiftly shot out to catch prey. The shell is reduced to a stiff **pen** embedded in the upper surface of the mantle. Adult size varies from tiny individuals of a few centimeters in length to the largest living invertebrate, the deep-sea colossal squid (*Mesonychoteuthis*). Very few specimens have been caught, but the largest, caught in 2007, had a total length of about 10 m (33 ft). The giant squid (*Architeuthis*) is another deep-sea squid. It may grow to 20 m (60 ft) in length but weighs less than the colossal squid.

Cuttlefishes (*Sepia*) resemble squids in having eight arms and two tentacles, but the body is flattened and has a fin running along the sides. Cuttlefishes, which are not fish at all, have a calcified internal shell that aids in buoyancy. This shell is the "cuttlebone" sold as a source of calcium for cage birds.

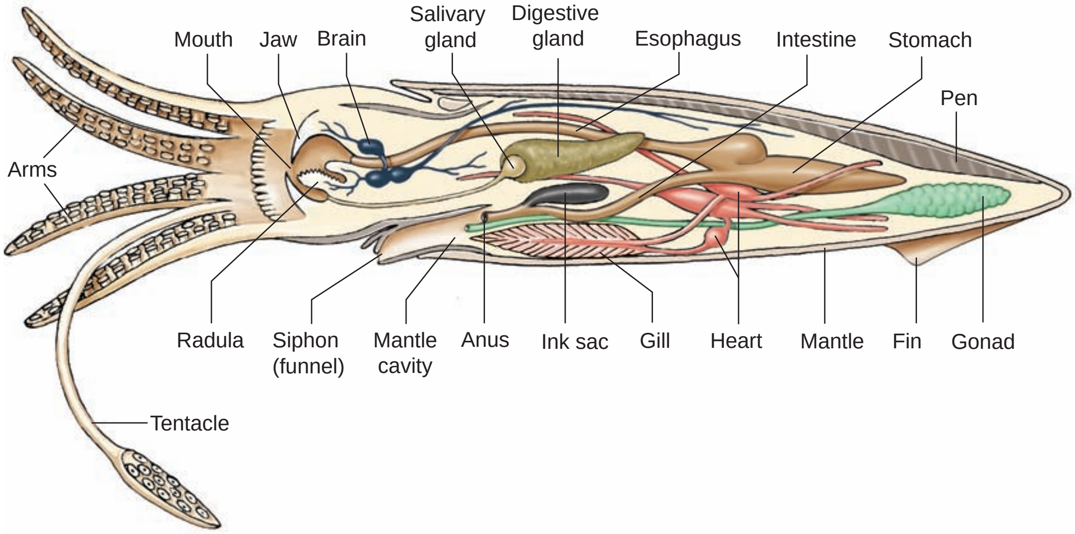
The chambered nautilus (*Nautilus;* see "The Chambered Nautilus," p. 360) has a coiled external shell containing a series of gas-filled chambers that serve as a buoyancy organ. The shell may be up to 25 cm (10 in.) in diameter. The body—which occupies the outer, largest chamber—has 60 to 90 short, suckerless tentacles used to capture prey.

Other Molluscs About 800 species of **chitons** (class **Polyplacophora**) are known, all marine. They can be readily identified by the eight overlapping shell plates that cover their slightly arched dorsal surface (Fig. 7.28). Their internal organs are not coiled as in snails.

Most chitons live on shallow, hard bottoms where they use a rasping radula to feed on algae. Many of them return to a homesite after feeding. One species, however, captures small crustaceans and other invertebrates with a flap-like extension of the mantle that surrounds the mouth.

The **monoplacophorans** (class **Monoplacophora**) are represented by only a handful of species of limpet-like molluscs. They were known only as fossils until the discovery of live individuals in 1952. They have now been collected, mostly from deep water, in scattered locations around the world. Monoplacophorans are peculiar because their gills and other organs are repeated along the body, which is reminiscent of the segmentation of annelids.

The 350 or so species of **tusk shells,** or **scaphopods** (class **Scaphopoda**), have an elongated shell, open at the top and tapered like an elephant tusk. They live in sandy or muddy bottoms. The narrow top end of the shell protrudes from the bottom, while the foot projects from the wide end. Many species



Juvenile *Illex illecebrosus*, Atlantic coast of North America

FIGURE 7.27 Section across a squid, showing its internal anatomy and only half the number of arms and tentacles.

EYE ON SCIENCE

The Sea Hare's Giant Nerve Cells

Aplysia californica, the California sea hare, has been used to study how the nervous system works. Humans and other vertebrates have billions of microscopic nerve cells, or neurons, electrically excitable cells involved in the transmission and storage of information. The sea hare, a shell-less gastropod, has only about 10,000, but they are giant-sized, and aggregate to form equally even larger ganglia. This is handy because it allows neurobiologists to easily identify and stimulate the sea here's individual nerve cells with microelectrodes or neurotransmitters. This makes it much easier to map the role of single nerve cells in specific functions in the nervous system than in the complex brain of vertebrates like rats and humans. The large size and simple organization of the sea hare's nerve cells have also helped in the study of the molecular events that take place during the transmission of nerve impulses.

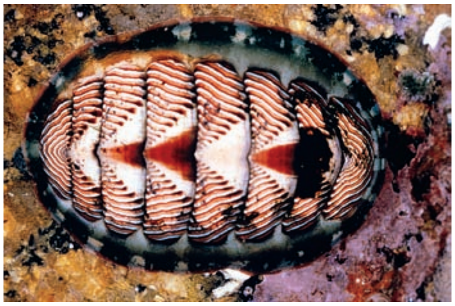
Research on *Aplysia* has been particularly useful in understanding the biological basis of learning and memory in which nerve cells play fundamental roles. Although its nervous system and behavior are relatively simple, *Aplysia* can learn simple tasks, and stores this information in nerve cells just as we do. In fact, Dr. Eric Kandel of Columbia University earned a share of the 2000 Nobel Prize in Medicine by using *Aplysia* for his research on the neurological basis of memory in the human brain.

Scientists have determined many of the *Aplysia* genetic sequences that control specific nerve cell functions, providing exciting links between gene expression, behavior, and learning. Researchers from the University of Florida and Columbia University analyzed gene expression in relation to nerve connections that control specific feeding and defensive behaviors. They discovered that more than 10,000 of the sea here's genes are active in a single nerve cell at any given time. This suggests that memory does not take place in isolation from other cellular functions. Most of these genes are unique to *Aplysia*, but surprisingly more than 100 are similar to genes associated with major neurological diseases in humans. These findings strongly suggest that the molecular and genetic basis for function of nerve cells in behavior and learning evolved early in animal evolution, and have remained relatively unchanged in diverse groups like molluscs and vertebrates, including humans.

Research is underway to complete sequencing the genome of *Aplysia californica*. The genome will reveal the complete set of genes that control or influence how nerve cells work. Since humans share some of these genes, application of this research may ultimately improve understanding of human learning and memory. It could also lead to treatments for Alzheimer's disease, some types of mental retardation, and at least some brain injuries.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

FIGURE 7.28 Chitons such as *Tonicella lineata* use their strong foot and the flexibility provided by the eight articulated shells to fit tightly to the irregular surface of rocky shores.



have thin tentacles with adhesive tips. They are used to capture **foraminiferans,** young bivalves, and other small organisms from the sediment. Tusk shells are most common in deep water, but empty shells sometimes wash ashore.

Biology of Molluscs

The body structure and organ systems of molluscs show a complexity that parallels their abundance and diversity.

Feeding and Digestion The molluscan gut has a separate mouth and anus. Digestion involves **salivary** and **digestive glands** (see Figs. 7.20 and 7.27) that release digestive **enzymes,** which break down food into simpler molecules. Other aspects of the digestive system differ among groups and according to diet.

Grazers such as chitons, limpets, and many snails have a rasping radula that removes minute algae from surfaces or cuts through large seaweeds. Their relatively simple digestive system can efficiently process large amounts of hard-to-digest plant material. Digestion is partly extracellular in the gut cavity and partly intracellular in the digestive glands. Some shell-less gastropods that feed on seaweeds keep the seaweeds' **chloroplasts** intact. The chloroplasts are kept in the digestive gland, where they can photosynthesize and provide nourishment for the gastropod.

Foraminiferans or Forams Protozoans with tiny calcareous shells.
- Chapter 5, p. 97; Figure 5.11

Enzymes Substances that speed up specific chemical reactions.
- Chapter 4, p. 65

Chloroplasts Cell organelles in plants and other primary producers in which the process of photosynthesis takes place.
- Chapter 4, p. 69; Figure 4.8*b*

Carnivorous snails have a radula modified to drill, cut, or even capture prey. The radula and mouth are contained in a proboscis that can be protruded to strike the prey (see Fig. 7.21). Jaws may even be present. In these snails digestion is extracellular and takes place in the stomach.

Bivalves ingest food particles that are filtered and sorted out by the cilia on the gills. The radula is absent, and food enters the mouth trapped in long strings of mucus. An enzyme-secreting rod in the stomach, the **crystalline style** (see Fig. 7.23*b*), continually rotates the food to help in its digestion. The stomach contents eventually pass into a large digestive gland for intracellular digestion. Giant clams not only filter food but also obtain nutrients from zooxanthellae living in tiny branches of the gut that extend into the clam's expanded mantle (see Fig. 14.34). This extra nourishment may allow the clams to attain their giant size.

All cephalopods are carnivores that have to digest large prey. The stomach is sometimes connected to a sac in which digestion is rapidly and efficiently completed. It is entirely extracellular.

Molluscs have a circulatory system that transports nutrients and oxygen. A dorsal, muscular heart pumps blood to all tissues. Most molluscs have an **open circulatory system** in which blood flows out of vessels into open blood spaces. Cephalopods, on the other hand, have a closed circulatory system in which the blood always remains in vessels and can be more effectively directed to oxygen-demanding organs such as the brain.

Nervous System and Behavior The nervous system of molluscs varies in complexity. Gastropods and bivalves do not have a single brain but, rather, several sets of **ganglia,** or "local brains," clusters of nerve cells located in different parts of the body (see Fig. 7.20; "The Sea Hare's Giant Nerve Cells," p. 133).

Cephalopods have the most complex nervous system not just of molluscs but of all invertebrates. Some of the separate local brains of other molluscs are fused into a single, large brain (see Figs. 7.25*c* and 7.27) that coordinates and stores information received from the environment. Different functions and behaviors of cephalopods are controlled by particular regions of the brain, as in humans. Giant nerve fibers rapidly conduct impulses, allowing cephalopods to capture prey or escape at amazing speeds. The strikingly complex eyes of cephalopods reflect the development of their nervous system. Octopuses and cuttlefishes have a remarkable capacity for learning. Most cephalopods, especially cuttlefishes, display color changes correlated with particular behaviors and moods, from intricate sexual displays to camouflage. Some cuttlefishes flash two large, black spots resembling eyes, perhaps to fool potential predators. Some octopuses even change color and behavior to mimic, or imitate, poisonous fishes and sea snakes!

Reproduction and Life History Most molluscs have separate sexes, but some species are **hermaphrodites,** animals in which individuals have both male and female gonads. In bivalves, chitons, tusk shells, and some gastropods, sperm and eggs are released into the water and fertilization is external (see Fig. 4.21*a*). Fertilization is internal in cephalopods and most gastropods. When cephalopods mate, the male uses a modified arm to transfer a **spermatophore,** an elongated packet of sperm, to the female. Males of gastropods that copulate have a long, flexible penis.

Some molluscs have a trochophore larva like polychaetes, a characteristic often used as evidence for close affinities among molluscs, the segmented worms, and other groups. In gastropods and bivalves the trochophore usually develops into a **veliger,** a planktonic larva that has a tiny shell (see Fig. 15.11*a*). In many gastropods, however, part or all of development takes place within strings or capsules of eggs. Cephalopods lack larvae, and the young develop from large, yolk-filled eggs. Female octopuses protect their eggs, which are often attached to crevices or holes in rocks, until they hatch. The female usually dies afterward because she eats little or nothing while guarding the eggs.

ARTHROPODS: THE ARMORED ACHIEVERS

Arthropods (phylum **Arthropoda**) make up the largest phylum of animals, with more than a million known species and several million remaining undiscovered. Of all the animals on earth, three out of four are arthropods. The largest group of arthropods by far, however, are the insects, which though the dominant arthropods on land are rare in the sea. The overwhelming majority of marine arthropods are **crustaceans** (subphylum **Crustacea**), a group that includes barnacles, shrimps, lobsters, crabs, and a huge variety of less familiar animals.

The arthropod body is segmented and bilaterally symmetrical. In addition to a flexible, segmented body arthropods have jointed appendages, such as legs and mouthparts, that are moved by sets of attached muscles. Another characteristic of arthropods is a tough, non-living external skeleton, or **exoskeleton,** composed of chitin and secreted by the underlying layer of tissue. The exoskeleton and jointed appendages provide protection, support, flexibility, and increased surface area for muscle attachment.

To grow, arthropods must **molt,** or shed their exoskeleton (Fig. 7.29). A new shell develops under the old one prior to molting, then hardens after the old skeleton is discarded and the animal takes in water to expand itself. Most arthropods are small because the rigid exoskeleton imposes limitations on size. We will never see arthropods as big as giant squids or whales, but the legs of a giant spider crab (*Macrocheira*) may reach 3 m (10 ft) long.

More species belong to the arthropods than to any other animal group. Most arthropods on land are insects, but crustaceans are the dominant arthropods in the sea. Arthropods have a segmented and bilaterally symmetrical body. Their success in adapting to all types of environments is due in part to a protective exoskeleton and jointed appendages.

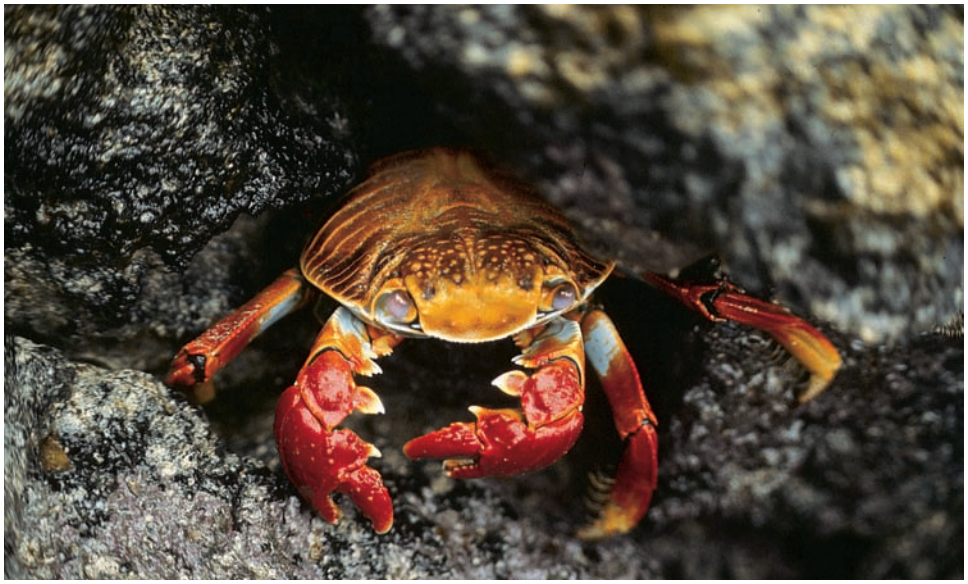


FIGURE 7.29 This is not really a live Galápagos shore crab (*Grapsus grapsus*) but its exoskeleton, or molt. The old exoskeleton covered the entire external surface of the crab, even its mouthparts and eyes. After molting, which is regulated by hormones, the soft, helpless crab must find shelter for a few days until its new, larger skeleton hardens.

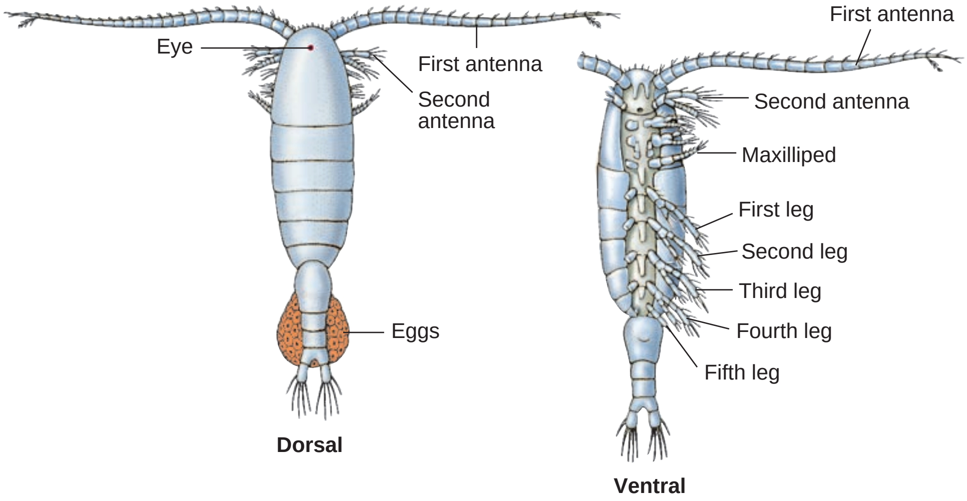


FIGURE 7.30 The structurally simplest crustaceans, like this planktonic copepod, tend to be small and have appendages that are similar to each other—that is, less specialized. One exception here is the first antenna, which is specialized for swimming (also see Figs. 15.6 and 15.7). All appendages are paired, but the ventral view shows only those on one side.

Crustaceans

There are approximately 68,000 known species of crustaceans, but there may be as many as 150,000 undescribed species. Most are marine.

Crustaceans are specialized for life in water, and most possess gills to obtain oxygen. Their chitinous skeleton is usually hardened by calcium carbonate. The appendages are specialized for swimming, crawling, attaching to other animals, mating, and feeding. Crustaceans possess two pairs of **antennae** (Figs. 7.30, 7.32, and 7.34), which are usually involved in sensing the surroundings. The crustacean body plan is repeated in myriad forms, from the familiar to the not-so-familiar.

Crustaceans are arthropods adapted for life in water. They have two pairs of antennae, gills, and a calcified exoskeleton.

The Small Crustaceans Small crustaceans are everywhere: in the plankton, on the bottom, among sediments, on and in other animals, and among seaweeds.

Copepods are extremely abundant and important in the plankton (see "Copepods," p. 332). They use their mouthparts to filter out or capture food. Some species are so common that they are among the most abundant animals on earth. Many planktonic species keep from sinking by using their enlarged first pair of antennae (Fig. 7.30) to swim. Many species are parasitic, some being so simplified that they look like little more than small bags of tissue.

Barnacles are filter feeders that usually live attached to surfaces, including living surfaces like whales and crabs. Many are very particular about the type of surface on which they live. Some are among the most important types of fouling organisms.

Common barnacles look almost like molluscs because their bodies are enclosed by heavy, calcareous plates (Fig. 7.31). The plates on the upper surface open to allow the feathery filtering appendages **(cirri),** which are actually the legs, to sweep the water. Some barnacles have become highly modified parasites and lack plates. All barnacles, however, have typical crustacean larvae, which swim and attach to surfaces before metamorphosing into adults (see Fig. 7.39).

Amphipods are small crustaceans with a curved body that is flattened sideways (Fig. 7.32). Most amphipods are under 2 cm (3/4 in) in length, but some deep-water species are much larger (see Fig. 16.26). The head and tail typically curve downward, and the appendages are specialized according to function. Beach hoppers, common in shore debris, are strong jumpers that spring about by briskly stretching their curved bodies. Other amphipods crawl among seaweeds. Burrowing in the skin of whales (as whale lice; see Fig. 10.9) and living as part of the plankton are some other lifestyles of this large, mostly marine group of over 5,000 species.

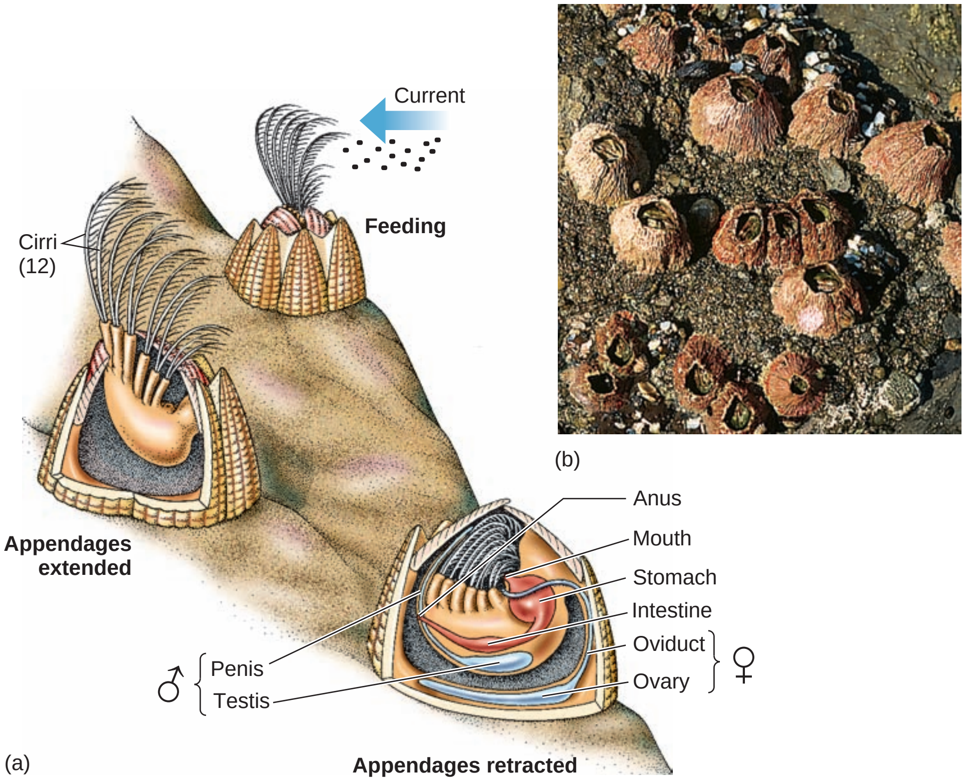


FIGURE 7.31 (*a*) Barnacles conceal a crustacean body beneath thick plates. They lie on their backs and use their legs to filter feed. Note that barnacles are hermaphrodites. Individuals, however, mate with each other, alternatively taking different sex roles. One individual may act as "male" by inserting its extended penis into a nearby "female." It may then turn into a "female" by accepting the penis of a neighbor. (*b*) The thatched barnacle (*Tetraclita squamosa*) from the Pacific coast of North America.

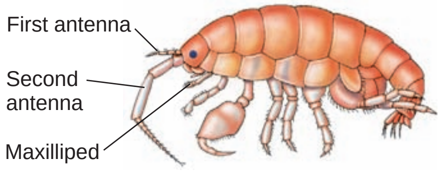


FIGURE 7.32 Most amphipods, like this beach hopper (*Orchestoidea*), can be recognized by a body that is curved and flattened sideways. The skeleton shrimps common among seaweeds and hydroids, however, are amphipods with bizarre skinny bodies. A giant deep-sea amphipod is illustrated in Figure 16.24.

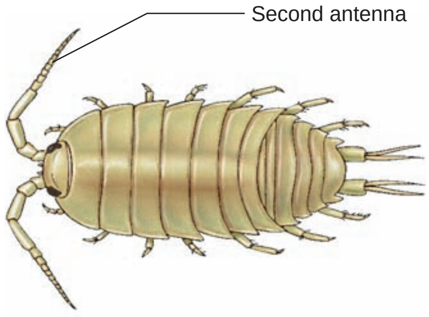


FIGURE 7.33 The sea louse, or sea roach (*Ligia oceanica*), is neither a louse nor a roach but an isopod. It feeds mainly on decaying seaweeds carried in to shore by the waves. Some isopods live as parasites on fishes (see Fig. 10.10).

Isopods are found in many of the same environments as amphipods. They are about the same size as amphipods, but isopods are easily identifiable because the main part of the body has legs that are similar to each other and the body is dorsoventrally flattened and thus has a flat back (Fig. 7.33). Pill bugs are common land isopods that are similar to many marine species. **Fish lice** (no relation to lice of birds and land mammals, which are insects) and other isopods are parasites of fishes (see Fig. 10.10) and other crustaceans.

Krill, or **euphausiids,** are planktonic, shrimp-like crustaceans up to 6 cm (2.5 in) long. The head is fused with some of the body segments to form a distinctive **carapace** that covers the anterior half of the body like armor (see Fig. 17.12). Most krill are filter feeders that feed on diatoms and other plankton. Krill are extremely common in polar waters, aggregating in gigantic schools of billions of individuals. They are an almost exclusive food source for many Antarctic whales, penguins, and fishes (see Fig. 10.14). Other species of krill live in the deep sea (see Fig. 16.2).

Shrimps, Lobsters, and Crabs With around 10,000 species, the **decapods** (the term means "10 legs") are the largest group of crustaceans. They include the shrimps, lobsters, and crabs. Decapods are also the largest crustaceans in size. Many are prized as food and are of great commercial importance.

Decapods feature five pairs of legs, or **pereopods,** the first of which is heavier and usually has claws used for feeding and defense (Fig. 7.34). Decapods also have three pairs of **maxillipeds,** which are closer to the mouth, turned forward, and specialized to sort out food and push it toward the mouth. Maxillipeds are used as filtering devices in decapods that eat small food particles. The carapace is well developed and encloses the part of the body known as the **cephalothorax.** The rest of the body is called the **abdomen.**

Shrimps and **lobsters** tend to have laterally compressed bodies with distinct and elongated abdomens, the "tails" we like to eat so much. Shrimps are typically **scavengers,** specialists in feeding on bits of detritus on the bottom. They also have other lifestyles. Many colorful shrimps, particularly in the tropics, live on the surface of other invertebrates (Fig. 7.35) or remove parasites from the skin of fish (see "Cleaning Associations," p. 218). Other shrimps live in deep water (see Fig. 16.2). Ghost and mud shrimps burrow in muddy bottoms (see Fig. 12.11). Lobsters, such as the American, or Maine, lobster (*Homarus;* Fig. 7.34) and the clawless spiny lobster (*Panulirus;* see Fig. 4.22) are mostly nocturnal and hide during the day in rock or coral crevices. They are scavengers and predators that crush molloscs and sea urchins.

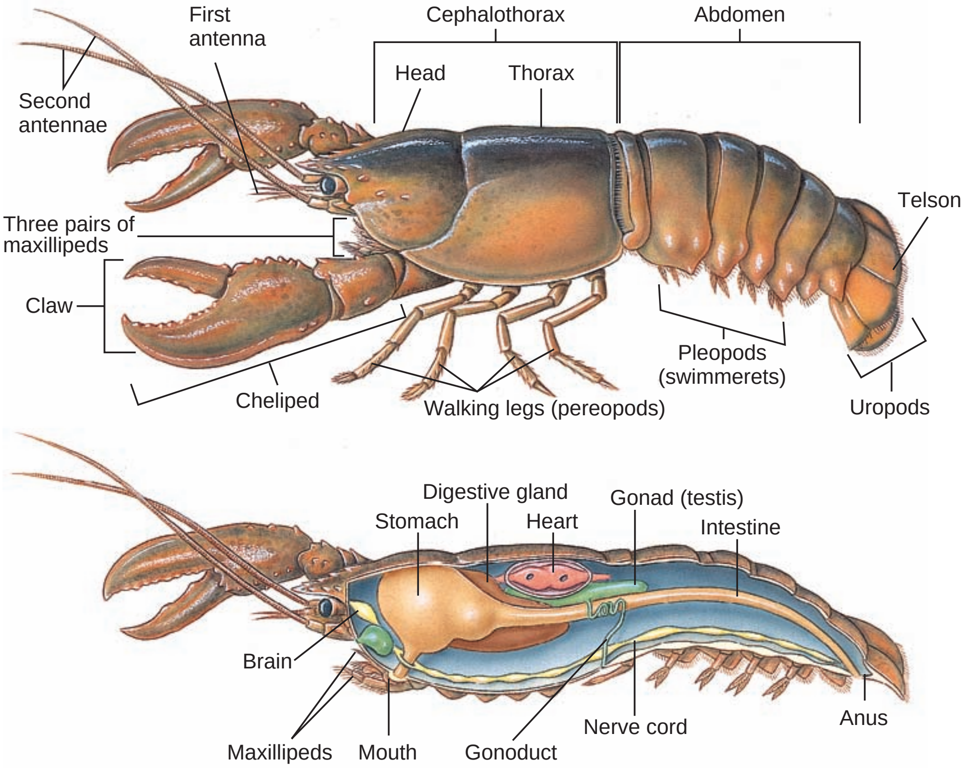


FIGURE 7.34 The American lobster (*Homarus americanus*) illustrates the basic body plan of decapod crustaceans. One significant omission from this drawing is the feathery gills, which lie in a chamber on each side of the cephalothorax. The ducts from the gonads, the gonoducts, open at the base of the last pair of walking legs in males and at the base of the second pair in females. Be sure to check next time you eat a lobster.

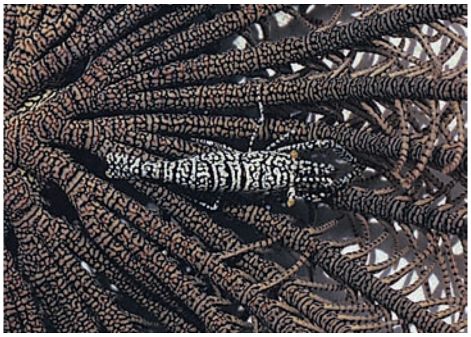


FIGURE 7.35 This shrimp (*Periclimenes*) is camouflaged to live on the branching arms of crinoids (see Fig. 7.47) in the tropical Pacific.

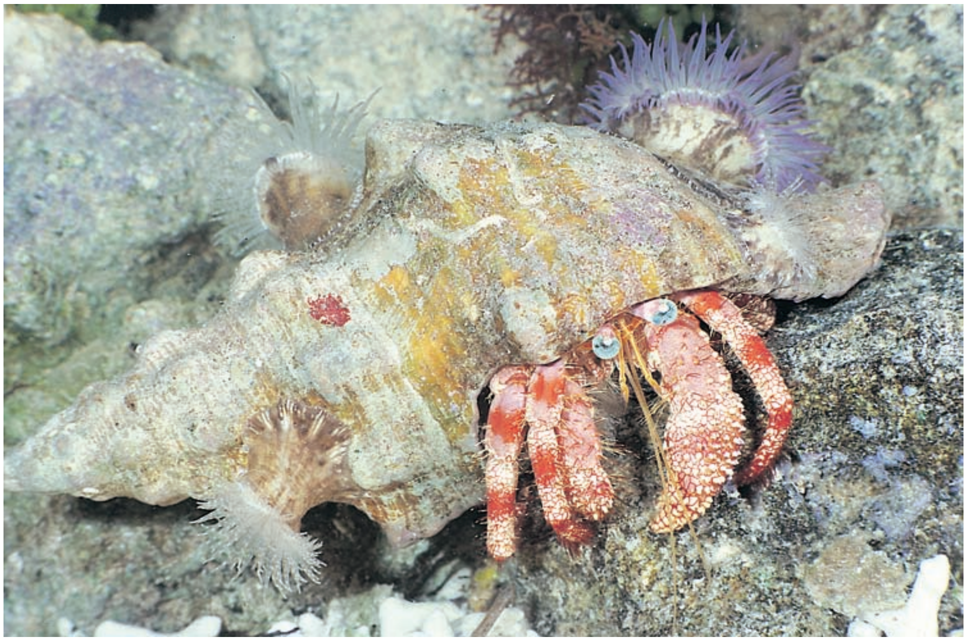


FIGURE 7.36 Hermit crab (*Dardanus* sp.) with sea anemones living on its shell. The hermit crab is protected by the nematocysts on the sea anemone's tentacles, and the sea anemones get to eat food particles that are let loose when the hermit crab feeds.

Hermit crabs, which are not true crabs, are also scavengers. They hide their long, soft abdomens in empty gastropod shells (see Fig. 10.5). Some hermit crabs cover their shells with sea anemones (Fig. 7.36) or sponges for added protection and camouflage. One type, however, doesn't hide its abdomen (Fig. 7.37).

In the **true crabs** the abdomen is small and tucked under the compact and typically broad cephalothorax. The abdomen is visible as a flat, **V**-shaped plate in males; in females it is expanded and **U**-shaped for carrying eggs (Fig. 7.38). Crabs may be highly mobile, and most can easily move sideways when in a hurry. They make up the largest and most diverse group of decapods, more than 4,500 species strong. Most are scavengers or predators, but some have specialized diets such as seaweeds, organic matter in mud, or even coral mucus (see the photo on page 115). Many crabs live along rocky shores or sandy beaches, exposed to air much of the time. Land crabs spend most of their lives on land, returning to the sea only to release their eggs.

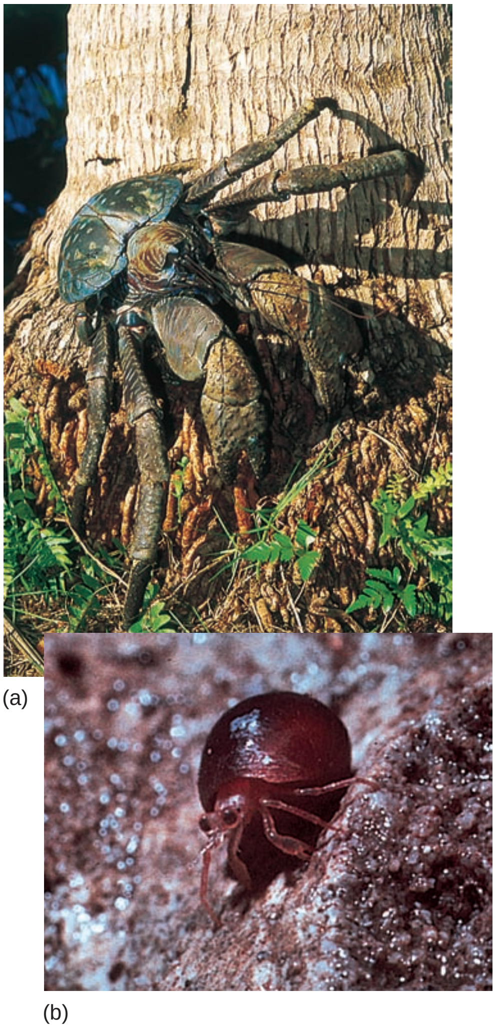
Biology of Crustaceans

The diversity of forms among crustaceans is paralleled by equally diverse functional features.

Feeding and Digestion Filter feeding is very common in copepods and many of the small planktonic crustaceans (see Fig. 15.7). Stiff, hair-like bristles on some appendages are used to catch food particles in the water. Particles are carried to the bristles by currents induced by the beating of other appendages. Still other specialized appendages move food from the bristles to the mouth. Appendages are adapted for piercing and sucking in parasitic copepods and isopods.

Food passes to a stomach that typically has chitinous teeth or ridges for grinding and bristles for sifting. The stomach,

FIGURE 7.37 The coconut crab (*Birgus latro*) is a large, land-dwelling hermit crab that does not use a shell as an adult (*a*). Females return to seawater only to release their eggs. After a planktonic existence, the young settle on the bottom and use shells for a home (*b*) as they crawl out of the sea to begin life on land. Coconut crabs, so called because they often eat coconuts, are found in the tropical Pacific and Indian oceans. They have been known to reach 13.5 kg (30 lb) in weight and are thus the largest and heaviest of all land arthropods.



(a)

(b)

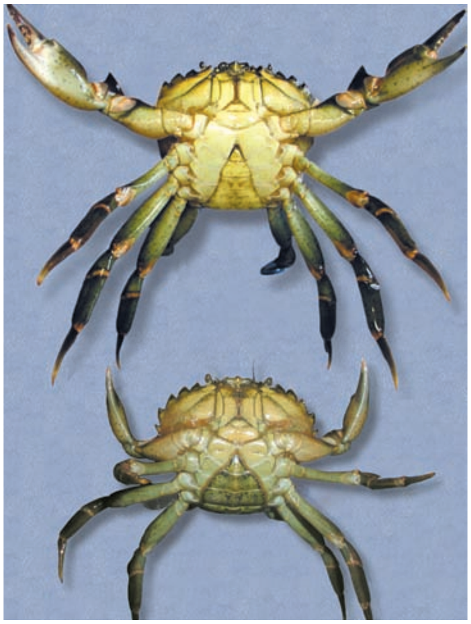
two-chambered in decapods, is connected to digestive glands that secrete digestive enzymes and absorb nutrients. Digestion is essentially extracellular. The intestine ends in an anus.

As in molluscs, absorbed nutrients are distributed by an open circulatory system. Gas exchange is typically carried out by gills attached to some of the appendages. In most decapods the gills lie in a chamber under the carapace, where they are constantly bathed by water. In land crabs, however, the gill chamber, though moistened, is filled with air and acts almost as our lungs do.

Nervous System and Behavior The nervous system of the structurally simplest crustaceans is ladder-like, but it is more centralized in decapods. Crustaceans have a small, relatively simple brain (see Fig. 7.34) but well-developed sensory organs. Most have **compound eyes,** which consist of a bundle of up to 14,000 light-sensitive units grouped in a mosaic. In decapods the compound eyes are at the end of movable stalks and can be used as periscopes. Crustaceans have a keen sense of "smell"—that is, they are very sensitive to chemicals in the water. Many crustaceans have a pair of statocysts for balance.

Crustaceans are among the most behaviorally complex invertebrates. They use a variety of signals to communicate with each other. Many of these signals involve special body postures or movements of the legs and antennae, which are often distinctively marked or colored to make the signals more conspicuous. This type of communication has been shown to be very important in settling disputes between neighbors and in courtship. Courtship behavior can be especially elaborate (see "Fiddler on the Mud," p. 273).

FIGURE 7.38 The abdomen is V-shaped in male crabs (top) and larger and U-shaped in females (bottom). This is the European, or shore, crab (*Carcinus maenas*), an introduced pest on the Atlantic and Pacific coasts of North America and other regions around the world.



Reproduction and Life History The sexes are separate in most crustaceans. Gametes are rarely shed into the water. Instead, males use specialized appendages to transfer sperm directly to the female. Even hermaphroditic species transfer sperm between individuals. Barnacles, for instance, have a penis that can stretch to reach other barnacles in the neighborhood. Mating in decapods usually takes place immediately after the female molts, while the exoskeleton is still soft. Females of many species can store sperm for long periods and use it to fertilize separate batches of eggs. In amphipods and isopods eggs are brooded in a chamber formed by lateral extensions of the body. In decapods and other groups females carry their eggs using **pleopods,** or swimmerets, specialized appendages beneath the body (see Fig. 7.34).

Most crustaceans have planktonic larvae that look nothing like the adult. Probably the most characteristic crustacean larva is the **nauplius,** but the type and number of larval stages vary widely from group to group (Fig. 7.39).

Other Marine Arthropods

Very few arthropods other than crustaceans are common in the ocean. Most belong to two small and entirely marine groups. A third group, huge and mostly terrestrial, includes a few shy invaders of the sea.

Horseshoe Crabs The **horseshoe crabs** are the only surviving members of a group (class **Merostomata**) that is widely represented in the fossil record. The five living species of horseshoe crabs are not true crabs but "living fossils," not unlike forms that became extinct long ago. Horseshoe crabs live on soft bottoms in shallow water on the Atlantic and Gulf coasts of North

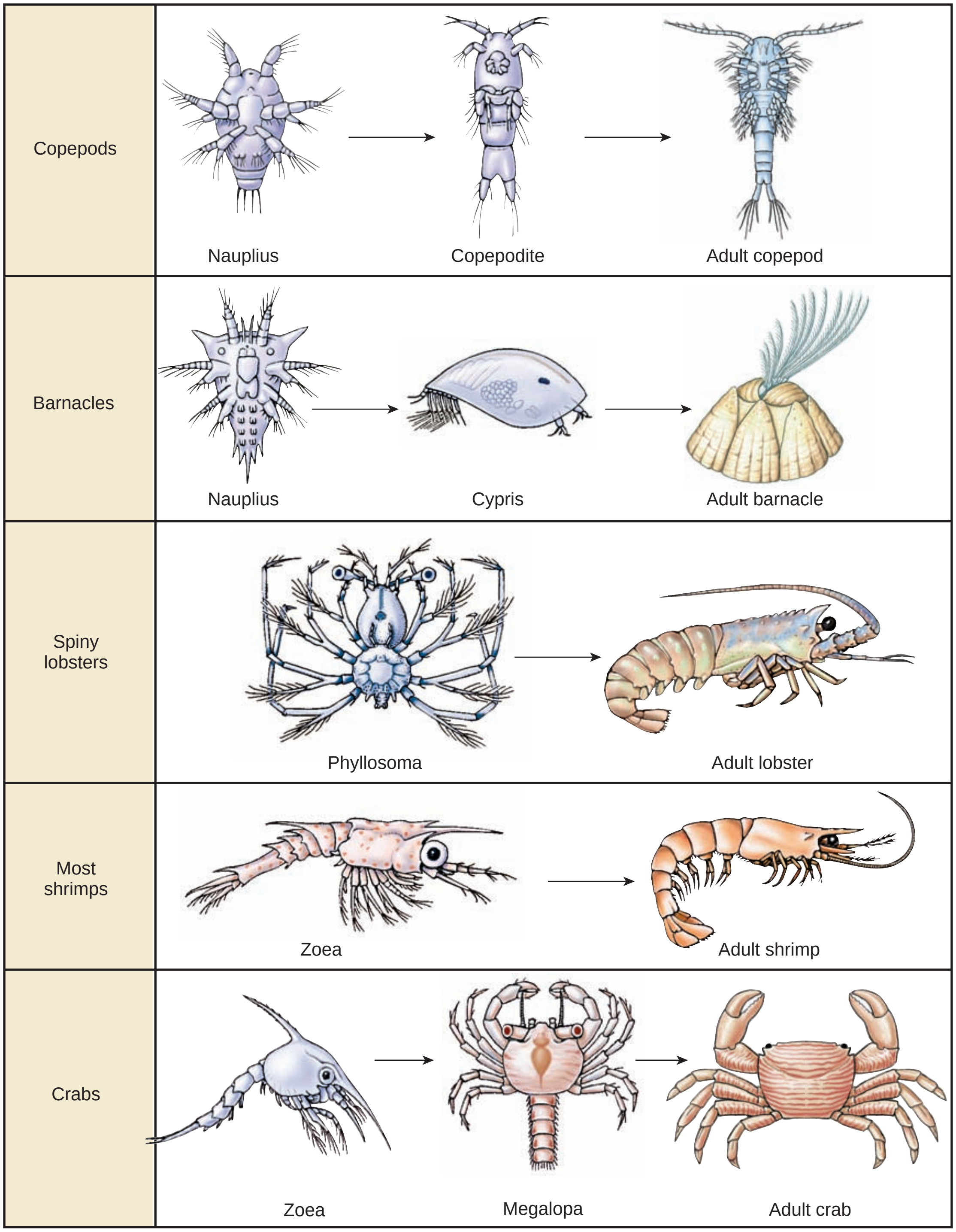

Copepods
Nauplius
Copepodite
Adult copepod
Barnacles
Nauplius
Cypris
Adult barnacle
Spiny lobsters
Phyllosoma
Adult lobster
Most shrimps
Zoea
Adult shrimp
Crabs
Zoea
Megalopa
Adult crab

FIGURE 7.39 The eggs of marine crustaceans hatch into planktonic larvae that undergo consecutive molts. Each molt adds a new pair of appendages, with the ones already present becoming more specialized. The last larval stage eventually metamorphoses into a juvenile (see Fig. 13.5). The larvae and adults shown here are not drawn to scale. In most cases, each arrow represents several molts. Other crustacean larvae are shown in Figure 15.13.

America (*Limulus*) and Southeast Asia (*Carcinoscorpius*). Their most distinctive feature is a horseshoe-shaped carapace that encloses a body with five pairs of legs (Fig. 7.40). They emerge on beaches to reproduce.

Sea Spiders **Sea spiders** (class **Pycnogonida**) only superficially resemble true spiders. Four or more pairs of jointed legs stretch from a small body (Fig. 7.41). A large proboscis with the mouth at the tip is used to feed on soft invertebrates such as sea anemones and hydrozoans. Sea spiders are most common in cold waters, but they occur throughout the oceans.

Insects **Insects** (class **Insecta**) are distinguished from other arthropods by having only three pairs of legs as adults. They are

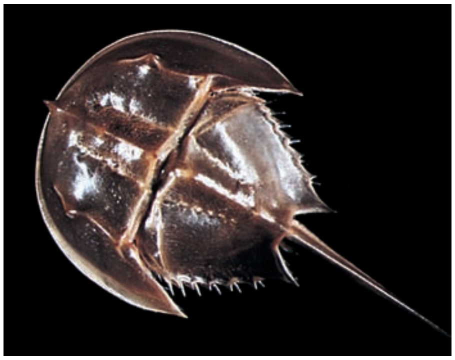


FIGURE 7.40 *Limulus polyphemus* is a horseshoe crab that grows as long as 60 cm (2 ft), including the tail. It feeds on clams and other small, soft-bottom invertebrates.

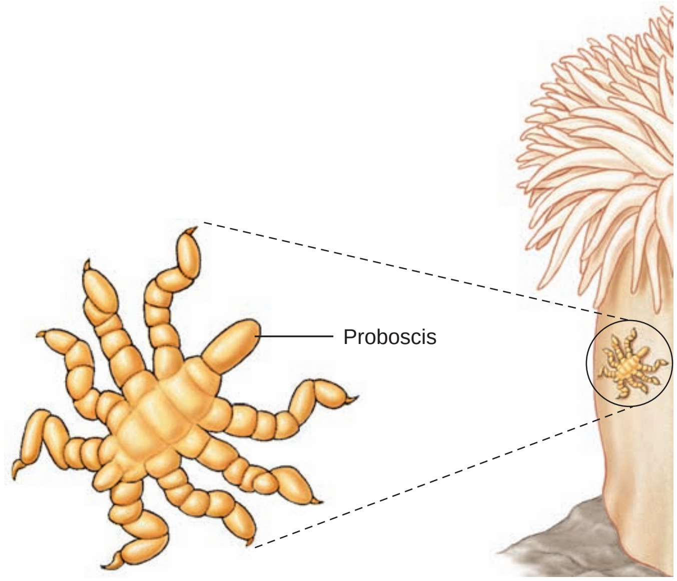


FIGURE 7.41 Sea spiders, or pycnogonids, are often found on soft-bodied invertebrates such as sponges, sea anemones, jellyfishes, and bryozoans. Most shallow-water species are small, with body length rarely over 1 cm (about ½ in.). Some deep-sea sea spiders are bigger, as are species in Arctic and Antarctic waters.

the most diverse group of animals on earth but are rare in the sea. Most marine insects live at the water's edge, where they scavenge among seaweeds, barnacles, and rocks. Many inhabit the decaying seaweed that accumulates at the high tide mark. One marine insect that is found far from shore is the marine water strider (*Halobates;* see Fig. 15.17).

LOPHOPHORATES

Three groups of marine invertebrates have a unique feeding structure, the **lophophore.** It consists of a set of ciliated tentacles arranged in a horseshoe-shaped, circular, or coiled fashion. Lophophorates are suspension feeders, using their cilia to create feeding currents. They share other important traits: lack of segmentation, bilateral symmetry, a coelom, and a **U**-shaped gut.

Bryozoans

Bryozoans ("moss animals") form colonies on seaweed, rocks, and other surfaces. Approximately 4,500 species, almost all marine, are grouped in the phylum **Ectoprocta.** Bryozoan colonies consist of minute interconnected individuals, called **zooids,** that secrete skeletons of a variety of shapes. The colonies may be encrusting or take an upright form that looks like tufts of crusty lace (Fig. 7.42). A close look reveals the rectangular, round, or vase-like compartments occupied by zooids (see Fig. 13.17). The lophophore is retractable. The **U**-shaped gut ends in an anus outside the edge of the lophophore.

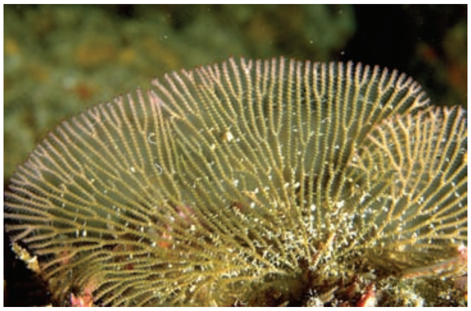


FIGURE 7.42 *Canda simplex* and many other bryozoans form crusty, lace-like colonies.

Phoronids

At first sight, **phoronids** (phylum **Phoronida**) may be easily confused with polychaetes. They are worm-like and build tubes made in part of sand grains. They have a horseshoe-shaped or circular lophophore, however, and their gut is **U**-shaped, in contrast to the straight gut of polychaetes. All 20 known species are marine, burrowing in sand or attaching their tubes to rocks and other hard surfaces in shallow water. Though one Californian species may reach 25 cm (10 in.), most phoronids are only a few centimeters long.

Lamp Shells

There are close to 350 living species of **lamp shells,** or **brachiopods** (phylum **Brachiopoda**). Thousands of other species are known only as fossils. Lamp shells have a shell with two valves, like the unrelated clams. The two valves are dorsal and ventral to the body, in contrast to the lateral (right and left) valves of clams. When the valves are opened, another major difference between lamp shells and clams is apparent. Lamp shells have a conspicuous lophophore, consisting of at least two coiled and ciliated arms, that occupies most of the space between the valves. Most brachiopods are found attached to rocks or burrowing in soft sediments.

ARROW WORMS

In terms of number of species, the **arrow worms,** or **chaetognaths** (phylum **Chaetognatha**), rank among the smallest animal phyla. Only about 100 species, all marine, are known. They are nevertheless one of the most common and important members of the plankton. They are almost transparent, streamlined, with fish-like fins and tail (Fig. 7.43). The head has eyes, grasping spines, and teeth. Total length ranges from a few millimeters to 10 cm (up to 4 in).

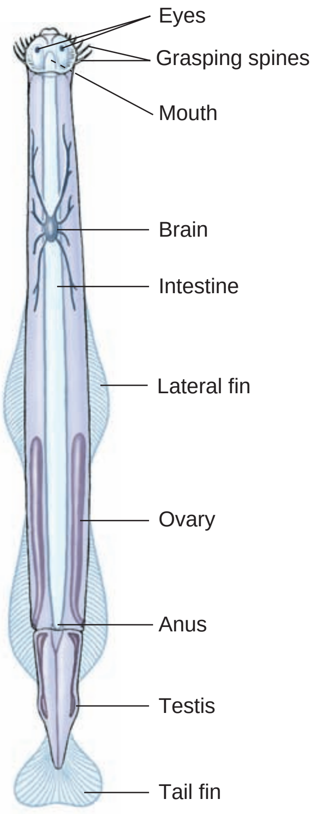

Eyes
Grasping spines
Mouth
Brain
Intestine
Lateral fin
Ovary
Anus
Testis
Tail fin

FIGURE 7.43 Arrow worms, or chaetognaths, have a transparent, fish-like body, an adaptation to living as planktonic predators. *Sagitta elegans* ("elegant arrow"), illustrated here, is widely distributed. Notice that individuals have both testes and ovaries.

Arrow worms are voracious carnivores with efficient sensory structures to detect their prey. They prey on small crustaceans, the eggs and larvae of fishes and other animals, other arrow worms, and practically anything else that is small. They spend most of their time motionless in the water but will swim in rapid, darting movements to grab their prey.

ECHINODERMS: FIVE-WAY SYMMETRY

Sea stars, sea urchins, sea cucumbers, and several other forms make up the **echinoderms** (phylum **Echinodermata**). Echinoderms are radially symmetrical, like cnidarians and comb jellies. The radial symmetry of echinoderms, however, is only a secondary development. Their planktonic larvae are bilaterally symmetrical (see Fig. 15.11*c*), and only the adults develop radial symmetry. Unlike cnidarians and comb jellies, echinoderms have **pentamerous** radial symmetry—that is, symmetry based on five parts (Fig. 7.44). As might be expected in a radially symmetrical animal, echinoderms lack a head. They have no anterior or posterior end or dorsal or ventral side. It is useful instead to refer to one surface of echinoderms as oral, because that is where the mouth is located, and the opposite surface as aboral (Fig. 7.44*a* and *b*).

Echinoderms typically have a complete digestive tract, a well-developed coelom, and an internal skeleton. This skeleton,

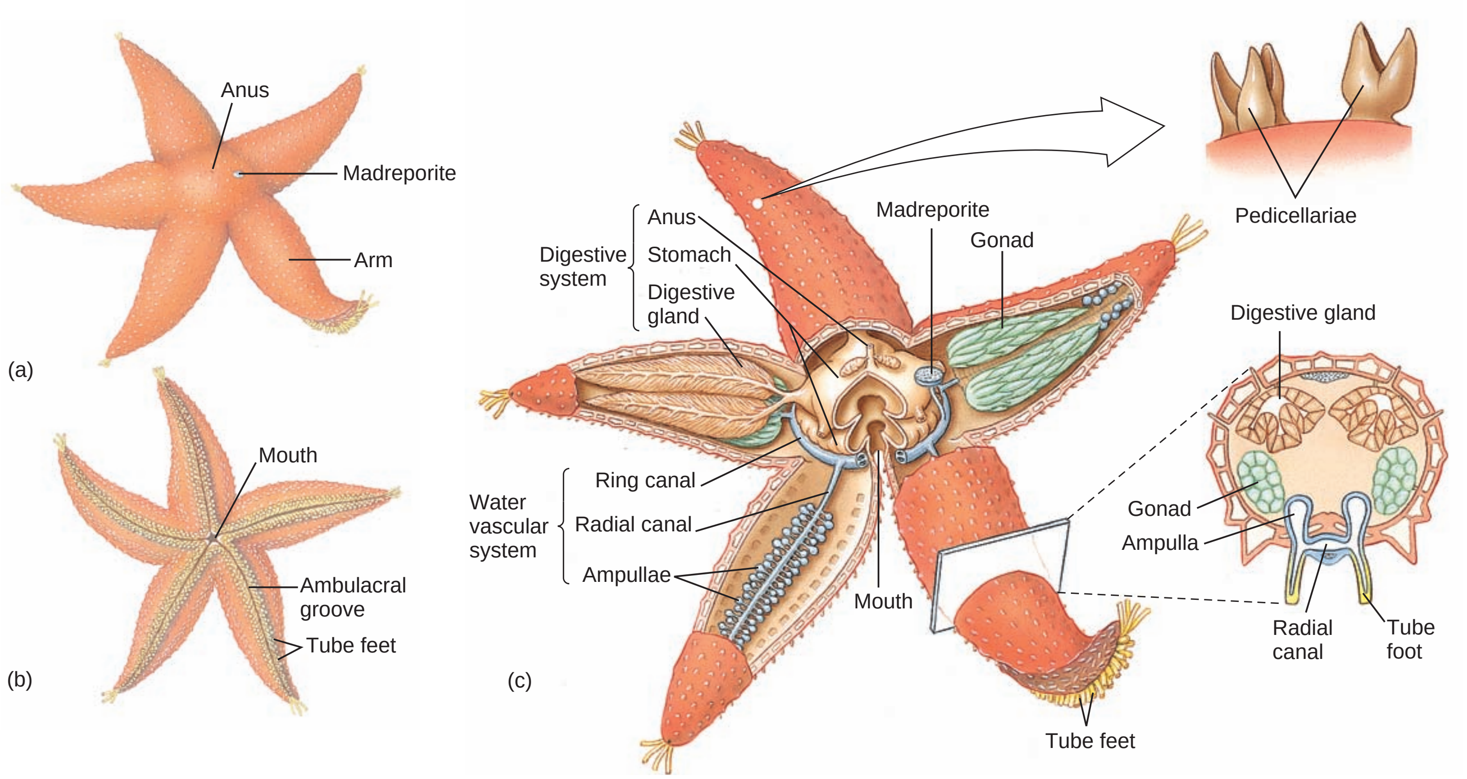

Anus
Madreporite
Arm
(a)
Mouth
Ambulacral groove
Tube feet
(b)
Digestive system
Anus
Stomach
Digestive gland
Madreporite
Gonad
Pedicellariae
Digestive gland
Water vascular system
Ring canal
Radial canal
Ampullae
Mouth
Gonad
Ampulla
Radial canal
Tube foot
Tube feet
(c)

FIGURE 7.44 (*a*) Aboral and (*b*) oral surfaces of a sea star (*Asterias vulgaris*) common on the Atlantic and Gulf coasts of North America. (*c*) Internal structure, with an arm cut across to show the relationship between tube feet, the internal sacs (ampullae), and the canals that make up the water vascular system. This and other carnivorous sea stars evert their thin-walled stomach and begin digesting prey without having to eat it.

like ours, is an **endoskeleton.** It is secreted within the tissues, rather than externally, like the exoskeleton of arthropods. Though sometimes it looks external, as in the spines of sea urchins, the endoskeleton is covered by a thin layer of ciliated tissue. Spines and pointed bumps give many echinoderms a spiny appearance—hence the name Echinodermata, meaning "spiny-skinned."

Unique to echinoderms is the **water vascular system,** a network of water-filled canals (Fig. 7.44*c*). **Tube feet** are muscular extensions of these canals. They are extended when filled with water, sometimes by the action of muscular sacs, the **ampullae,** that extend inside the body opposite the tube feet. Tube feet often end in a sucker and are used for attachment, locomotion, and the reception of chemical and mechanical stimuli. In sea stars and sea urchins (see Fig. 7.48) the system connects to the outside through the **madreporite,** a porous plate on the aboral surface.

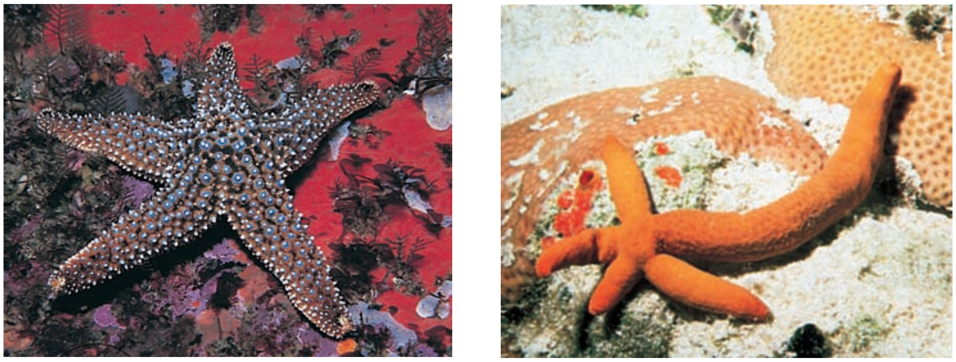


FIGURE 7.45 (*a*) The giant spined sea star (*Pisaster giganteus*) from the Pacific coast of North America. (*b*) *Linckia guildingi*, from the Caribbean, shows a remarkable ability for regeneration; here the larger arm regenerated the central disk and four small arms to form a complete individual.

Echinoderms are radially symmetrical as adults. They are characterized by an endoskeleton and a unique water vascular system.

Types of Echinoderms

The echinoderms are a large group of about 7,000 known species, all marine. They are important members of bottom communities from the poles to the tropics.

Sea Stars **Sea stars** (class **Asteroidea**), sometimes called starfishes, clearly display the distinctive echinoderm body plan (Fig. 7.44). Most species have five arms that radiate from a central disk, though some have more than five, sometimes close to 50. Hundreds of tube feet protrude from the oral surface along radiating channels on each arm called **ambulacral grooves** (Fig. 7.44*b*). Sea stars can move in any direction, though usually slowly, by reaching out their tube feet and pulling themselves along.

The endoskeleton of sea stars consists of interconnected calcium carbonate plates that form a relatively flexible framework. This allows their arms to be somewhat flexible. The aboral surface of many sea stars is often covered with spines modified into minute, pincer-like organs called **pedicellariae** (Fig. 7.44*c*). They help keep the surface clean.

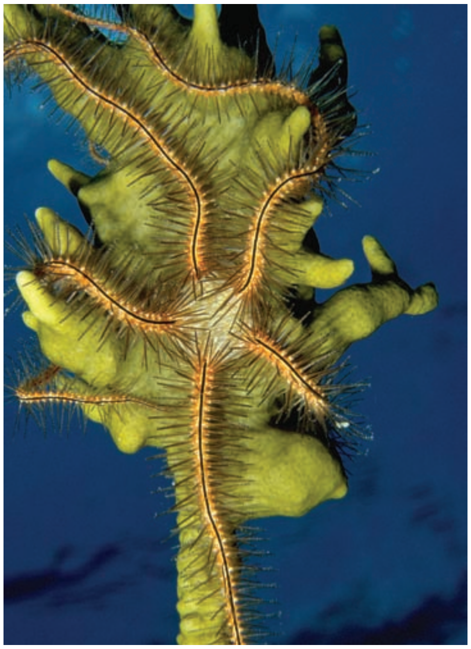


FIGURE 7.46 *Ophiothrix oerstedii* is a brittle star typically found on sponges and other habitats in the Caribbean.

Most sea stars are predators of bivalves, snails, barnacles, and other attached or slow-moving animals. Typical examples include *Asterias* (Fig. 7.44), common on rocky shores from the North Atlantic to the Gulf of Mexico, and *Pisaster* (Fig. 7.45*a*), its counterpart on the North Pacific.

Brittle Stars **Brittle stars** (class **Ophiuroidea**) also have a star-shaped body architecture. The five arms, however, are long, very flexible, and sharply demarcated from the central disk (Fig. 7.46). The swift, snake-like movements of the arms are used in locomotion. The tube feet, which lack suckers, are used in feeding. Unlike sea stars, the gonads and other internal organs of brittle stars are contained within the central disk and do not extend into the arms.

Most brittle stars eat detritus and small animals they pick up from the bottom of the water. Particles are collected by the tube feet and passed from foot to foot to the mouth. They lack an anus. There are more species of brittle stars, around 2,000, than of any other group of echinoderms. Brittle stars are widely distributed but not always visible, often hiding under rocks and corals or covering themselves with mud or sand.

Sea Urchins In **sea urchins** (class **Echinoidea**) the endoskeleton forms a round, rigid, shell-like test with movable spines and pedicellariae (Figs. 7.47 and 7.48). Locomotion is achieved by the movable spines, jointed to sockets in the test, and the sucker-tipped tube feet. The flat and radiating body plan of sea stars can be transformed into a sea urchin by dropping the arms and pulling the oral and aboral surfaces to form a sphere. The five rows of ambulacral grooves with their tube feet now extend along the outer surface of the sphere (Fig. 7.48). The mouth is on the bottom and the anus on top. The plates that make up the test can be seen in a sea urchin cleaned of spines

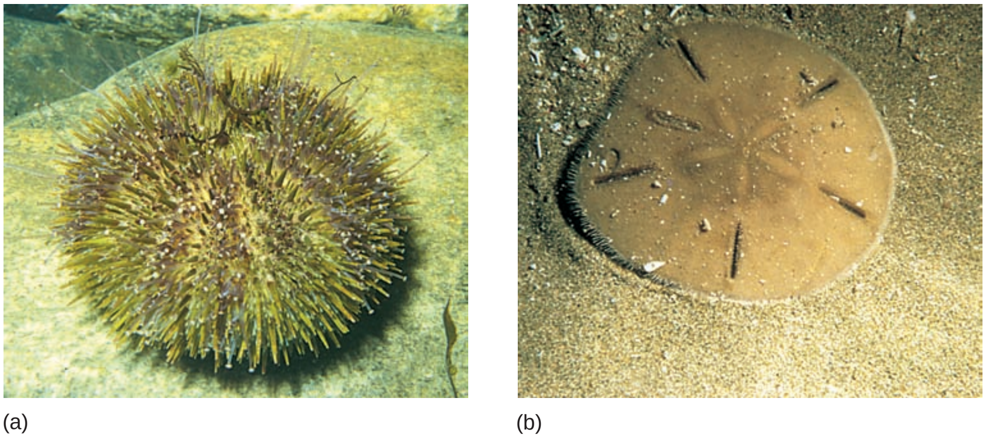


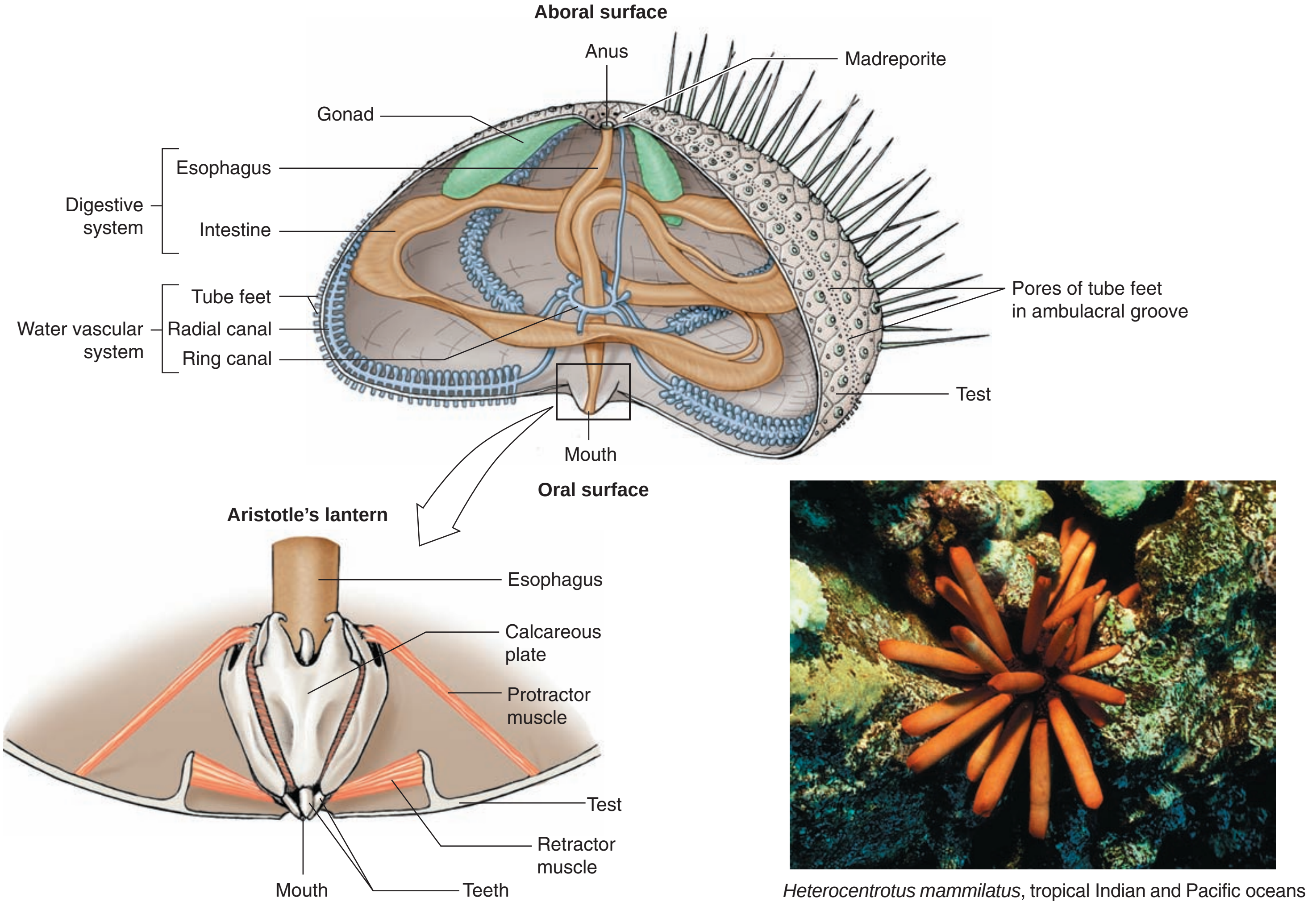
FIGURE 7.47 (*a*) The green sea urchin (*Strongylocentrotus droebachiensis*) is found on rocky shores and kelp forests on the Atlantic, Arctic, and Pacific coasts of North America. (*b*) *Mellita sexiesperforata*, the six-hole sand dollar from sandy bottoms along the southern United States and the Caribbean. The five-part pattern characteristic of all echinoderms can be seen in the light star pattern in the center of the sand dollar.

and tissue. Bands of pores along the ambulacral grooves correspond to the bands of tube feet.

Sea urchins graze on attached or drifting seaweeds and seagrasses. In the process they also ingest detritus and encrusting animals such as sponges and bryozoans. The mouth, directed downward, has an intricate system of jaws and muscles called **Aristotle's lantern** (Fig. 7.48), which is used to bite off algae and other bits of food from the bottom.

Sea urchins are a common sight on rocky shores throughout the world. Examples are species of *Arbacia* from the Atlantic Ocean and Gulf of Mexico and *Strongylocentrotus* from most North Atlantic and Pacific coasts (Figs. 7.47*a* and 13.19). Sea urchins in the tropics show an even richer variety of shapes and sizes, particularly on coral reefs (*Echinometra, Diadema;* see Fig. 14.33).

Not all of the approximately 1,000 species in the class Echinoidea have round tests with prominent spines. **Heart urchins** (see Fig. 13.7) and **sand dollars** (Figs. 7.47*b* and 13.8) are adapted to live in soft bottoms by having flattened bodies and short spines. They are deposit feeders that use their tube feet and sometimes strands of mucus to pick up organic particles.


Aboral surface
Anus
Madreporite
Gonad
Esophagus
Digestive system
Intestine
Tube feet
Water vascular system
Radial canal
Ring canal
Pores of tube feet in ambulacral groove
Test
Mouth
Oral surface
Aristotle's lantern
Esophagus
Calcareous plate
Protractor muscle
Test
Retractor muscle
Mouth
Teeth

Heterocentrotus mammilatus, tropical Indian and Pacific oceans

FIGURE 7.48 Internal structure of a typical sea urchin, with a simplified diagram of the Aristotle's lantern. Five pairs of protactor muscles push the lantern down, exposing the teeth; five pairs of retractor muscles move the lantern and teeth in. Additional muscles are responsible for grasping and other movements of the teeth.

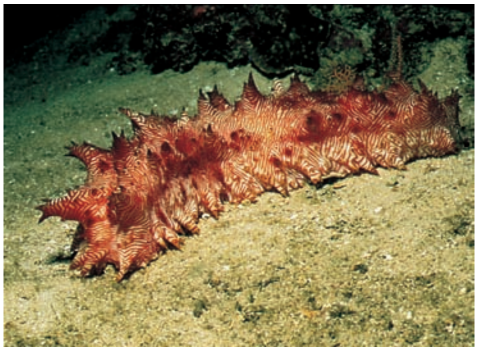


FIGURE 7.49 A sea cucumber (*Thelenota rubralineata*) from Papua New Guinea. Sea cucumbers in general are among the largest echinoderms, reaching 2 m (6.6 ft) in length.

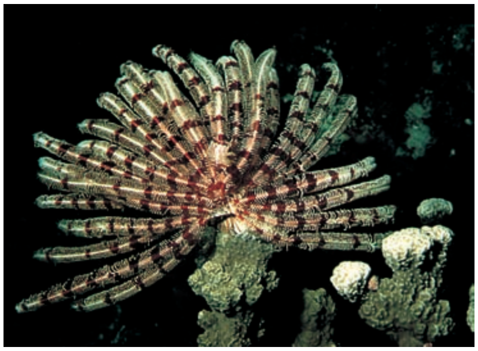


FIGURE 7.50 A feather star, or crinoid, photographed at night at Kwajalein atoll, Marshall Islands. The outstretched arms of feeding individuals can reach a diameter of 70 cm (more than 2 ft). See Figure 7.35 for a close-up of arms.

Sea Cucumbers In yet another modification of the echinoderm body plan, **sea cucumbers** (class **Holothuroidea**) are superficially worm-like (Fig. 7.49). They do not have spines and lack an obvious radial symmetry. The basic body plan of sea urchins appears to have been elongated along the oral-aboral axis, as if they were pulled from the mouth and anus and stretched. The animal lies on one side, where the five rows of tube feet are concentrated. The oral and aboral surfaces are at the ends. The endoskeleton consists of microscopic, calcareous spicules scattered throughout the warty, often tough skin. Like sea urchins, most species have five rows of tube feet extending from mouth to anus.

Many sea cucumbers are deposit feeders. The tube feet around the mouth are modified into branched tentacles that are used to pick up organic matter from the bottom or scoop sediment into the mouth (see Fig. 7.3). Some sea cucumbers burrow or hide and extend only their tentacles to obtain food directly from the water.

Many sea cucumbers have evolved novel defensive mechanisms that compensate for the lack of a test and spines. Some secrete toxic substances. When disturbed, some species discharge sticky, sometimes toxic filaments through the anus to discourage potential predators. Others resort to a startling response, the sudden expulsion of the gut and other internal organs through the mouth or anus, a response known as **evisceration.** It is assumed that evisceration distracts the offender while the sea cucumber, which will eventually grow back the lost organs, escapes—messy, perhaps, but effective.

Crinoids Crinoids (class **Crinoidea**) are suspension feeders that use outstretched, feathery arms to obtain food from the water. Crinoids are represented by close to 600 species of **feather stars** (Fig. 7.50) and **sea lilies.** Sea lilies are restricted to deep water and attach permanently to the bottom. Feather stars perch and crawl on hard bottoms in both shallow and deep waters, especially in the tropical Pacific and Indian oceans. They are also capable of graceful swimming.

The body plan of crinoids is best described as an upside-down brittle star with the ambulacral grooves and mouth directed upward. The mouth and larger organs are restricted to a small, cup-shaped body from which the arms radiate. Some crinoids have only five arms but most have many—up to 200—because of branching of the initial five. The arms also have small side branches (see Fig. 7.35). Tiny tube feet along these side branches secrete mucus, which aids in catching food particles. Food makes its way into the mouth by way of ciliated ambulacral grooves. These appendages tilt the body, so that the extended arms orient to currents for efficient suspension feeding.

Biology of Echinoderms

Radial symmetry is associated with sedentary lifestyles. With the exception of limited swimming in some feather stars and some deep-water sea cucumbers, adult echinoderms are relatively slow bottom crawlers. But do they need to be fast to be successful? Certainly not.

Feeding and Digestion The digestive system of echinoderms is relatively simple. Most sea stars are carnivorous. Many feed by extending, or everting, part of their stomach inside out through the mouth to envelop the food. The stomach then secretes digestive enzymes produced by large digestive glands that extend into the arms (Fig. 7.44*c*). The digested food is carried into the glands for absorption and the stomach pulled back inside the body. The intestine is short or missing. Brittle stars and crinoids also have simple, short guts. Brittle stars lack an anus.

The gut of sea urchins and sea cucumbers is long and coiled (Fig. 7.48). In sea urchins this is an adaptation for the lengthier digestion needed for the breakdown of plant material. A long gut also is advantageous to sea cucumbers because they need to process large amounts of sediment to obtain enough organic matter.

In all echinoderms nutrients are transported in the fluid that fills the extensive body cavity. The fluid is called **coelomic fluid** because the body cavity of echinoderms is a coelom.

The coelomic fluid also transports oxygen because most echinoderms lack a distinct circulatory system. In sea stars and sea urchins gas exchange takes place across small, branched projections of the body wall connected at the base to the coelomic cavity. In sea cucumbers water is drawn in through the anus into a pair of thin, branched tubes called **respiratory trees.** The respiratory trees are extensions of the gut and are suspended in the body cavity, surrounded by coelomic fluid. They provide a large surface area in close proximity to the coelomic fluid, thus allowing considerable gas exchange.

Nervous System and Behavior Our knowledge of the nervous system of echinoderms is rather limited. The presence of a nerve net is reminiscent of cnidarians. The nervous system coordinates movements of tube feet and spines in the absence of a brain. Nevertheless, more complex behaviors, such as the righting of the body after being turned over and camouflaging with bits of debris by sea urchins, are evidence that the nervous system may not be as simple as it looks.

Reproduction and Life History The sexes are separate in most echinoderms. In most groups, 5, 10, or more gonads shed sperm or eggs directly into the water. The gonads are usually located in the body cavity and open to the outside by way of a duct (see Figs. 7.44*c* and 7.48). Gametes do not survive long in the water, so in many species individuals spawn all at once to ensure fertilization.

Development of the fertilized egg proceeds in the plankton and typically results in a ciliated larva characteristic of each group (see Fig. 15.11*b* and *c*). Echinoderm larvae are bilaterally symmetrical and it is not until metamorphosis that radial symmetry develops. Some echinoderms do not have planktonic larvae and brood their offspring in special pouches or under the body.

Some sea stars, brittle stars, and sea cucumbers regularly reproduce asexually by the separation of the central disk or body into two pieces. The resulting halves then grow into complete individuals. **Regeneration,** the ability to grow lost or damaged body parts, is highly developed in echinoderms. Sea stars, brittle stars, and crinoids regenerate lost arms. In some sea stars a severed arm can grow into a new individual (see Fig. 7.45*b*). Efforts to control sea stars that prey on oyster beds or corals by cutting them up and throwing the pieces back into the water have failed miserably. In most sea stars, however, only arms that include portions of the central disk can regenerate.

HEMICHORDATES: A "MISSING LINK"?

The search for evolutionary links between the chordates—our own phylum—and other groups of animals (see Fig. 7.54) has been a provocative challenge, and several explanations have been proposed. As strange as it may seem, echinoderms and chordates share several features related to the development of our embryos. The wide evolutionary gap between echinoderms and chordates, however, may be filled by a small and infrequently seen group of worms, the **hemichordates** (phylum **Hemichordata**). Hemichordates share the same basic developmental characteristics of chordates and echinoderms. Some hemichordates also have a larva similar to that of some echinoderms. Hemichordates share with us chordates some of the features used to define our phylum. These characteristics—a dorsal, hollow nerve cord and openings along the anterior part of the gut—will be discussed in the following section.

The hemichordates include 85 known species. Most of these are **acorn worms,** or **enteropneusts,** worm-like deposit feeders that live free or in **U**-shaped tubes. Some acorn worms have been found around hydrothermal vents, often in large numbers. They generally range in length from about 8 to 45 cm (3 to 18 in) but some reach 2.5 m (more than 8 ft). Like sea cucumbers, practically all acorn worms ingest sediment, using a thick, mucus-secreting proboscis to collect organic material, which is then swept toward the mouth.

CHORDATES WITHOUT A BACKBONE

The **chordates** (phylum **Chordata**) are divided into three major groups, or subphyla. Two of these lack a backbone and are discussed here with the invertebrates. These invertebrate chordates are collectively called **protochordates.** The third and by far the largest chordate subphylum comprises the vertebrates, the subject of Chapters 8 and 9.

The estimated 49,000 living species of chordates share many characteristics, but four stand out. During at least part of their development, all chordates, including humans, have (1) a single, hollow **nerve cord** that runs along the dorsal length of the animal, (2) **gill** (or **pharyngeal**) **slits,** small openings along the anterior part of the gut (or **pharynx**), (3) a **notochord,** a flexible rod for support that lies between the nerve cord and the gut, and (4) a **post-anal tail**—that is, a tail that extends beyond the anus (Figs. 7.51*b* and 7.53). All chordates also have a ventral heart. In vertebrates the notochord is surrounded or replaced by a series of articulating bones, the **backbone,** or vertebral column.

All chordates possess—at least during part of their lives—a dorsal nerve cord, gill slits, a notochord, and a post-anal tail. Vertebrate chordates also have a backbone.

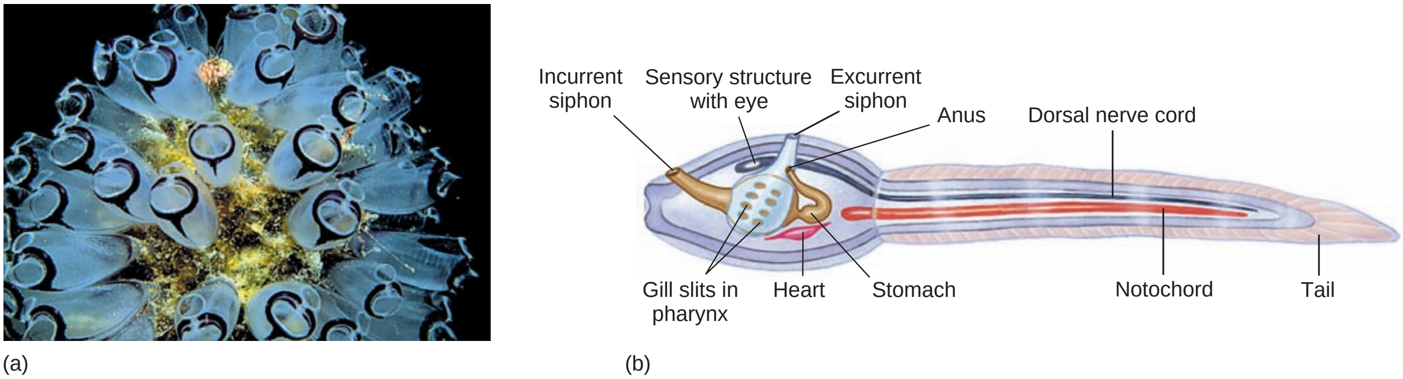


FIGURE 7.51 (*a*) *Clavelina picta* is a colonial sea squirt, or ascidian. Its outer covering, the tunic, contains cellulose, a substance typical of plants. (*b*) The tadpole larva of ascidians exhibits all the distinguishing characteristics of chordates. Some of these characteristics, however, are missing in the adults.

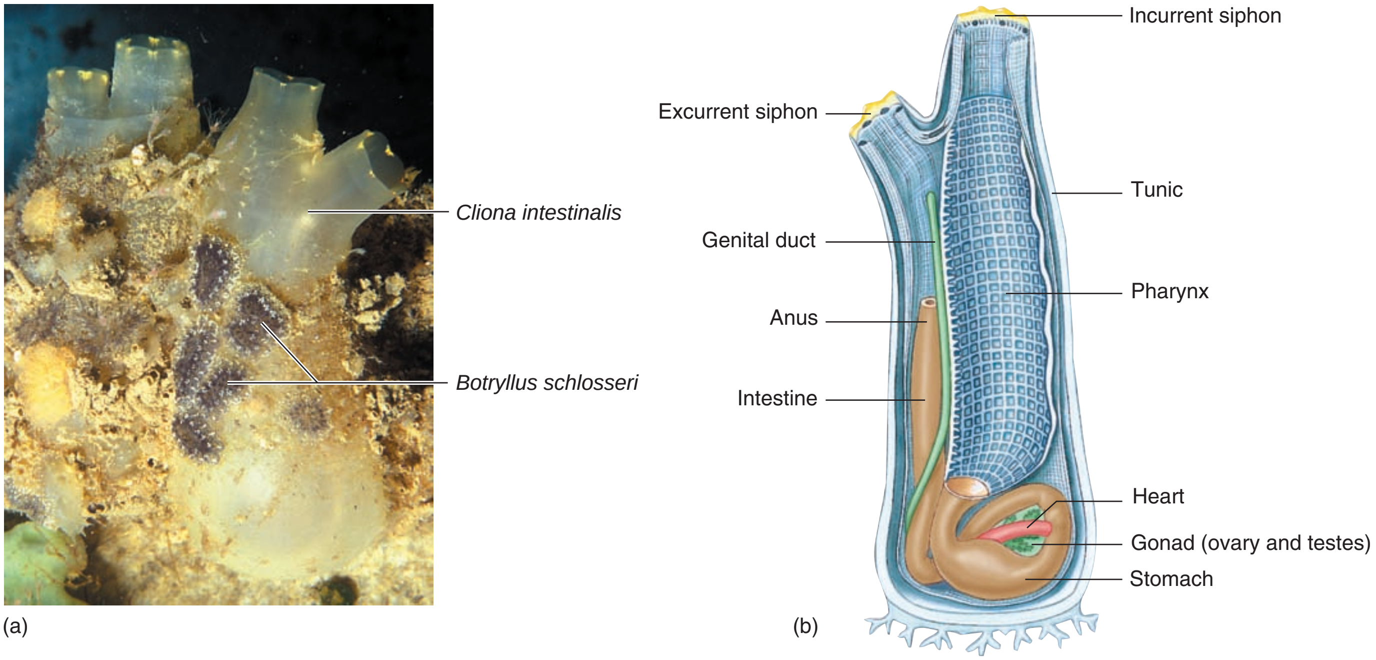


FIGURE 7.52 *Cliona intestinalis* is a shallow-water sea squirt that has become a common fouling animal in many parts of the world. A colonial sea squirt (*Botryllus schlosseri*) can be seen on the outer covering, or tunic, of *Cliona* (*a*).

Tunicates

The largest group of protochordates is the **tunicates** (subphylum **Urochordata**). All 3,000 known species are marine. Those we are most apt to see are the **sea squirts,** or **ascidians** (class **Ascidiacea**). Their sac-like bodies are attached to hard surfaces, often as fouling organisms (Fig. 7.52*a*), or anchored in soft sediments. They are the only sessile, or permanently attached, chordates. To the inexperienced eye, some sea squirts may be confused with sponges because of their general appearance. The body of the sea squirt, however, is protected by a **tunic,** a leathery or gelatinous outer covering that often has a different texture than that of sponges, and the internal structure is completely different (Fig. 7.52*b*).

Sea squirts are filter feeders. Water typically flows through the mouth, or **incurrent siphon,** and is filtered by a ciliated, sieve-like sac. This sac represents the pharynx, and the openings are derived from the gill slits. Food is filtered from the water and passed into a U-shaped gut. Filtered water is expelled through a second opening, the **excurrent siphon.** When disturbed or expelling debris, ascidians force a jet of water out of both siphons, giving them their common name of sea squirts. Some sea squirts are colonial, some consisting of clumps of separate individuals (Fig. 7.51*a*) and others of a circular, flower-like arrangement of individuals having a common tunic and excurrent siphon (Figs. 7.52*a* and 13.17).

Were it not for their planktonic larvae, the headless, attached sea squirts could easily pass as anything but chordates. The adults possess neither a notochord nor a dorsal nerve cord (Fig. 7.52*b*). Ascidian larvae are known as **tadpole larvae** because of their superficial resemblance to the tadpoles of frogs (Fig. 7.51*b*). Tadpole larvae clearly display the fundamental chordate traits. They have gill slits, a dorsal nerve cord, a notochord, and a well-developed post-anal tail. They also have an eye. Tadpole larvae do not feed; their only purpose is to find a suitable surface on which to settle. During metamorphosis of a tadpole larva into a juvenile ascidian, the notochord and tail are reabsorbed and free existence is no more.

Some tunicates lead a planktonic existence throughout their lives. **Salps** (class **Thaliacea**) have a transparent, barrel-shaped body with muscle bands for locomotion (see Fig. 15.8). Water enters through the anterior mouth, or incurrent siphon, and is forced out through the excurrent siphon on the posterior end. Salps can be extremely abundant, particularly in warm water. Some are colonial, much like floating colonies of sea squirts, and may reach several meters in length. **Larvaceans,** or **appendicularians** (class **Larvacea**) are another group of planktonic tunicates. They retain the body of a tadpole larva through life. Each tiny individual secretes a complex but delicate gelatinous "house" for protection and to filter water for food (see Fig. 15.9).

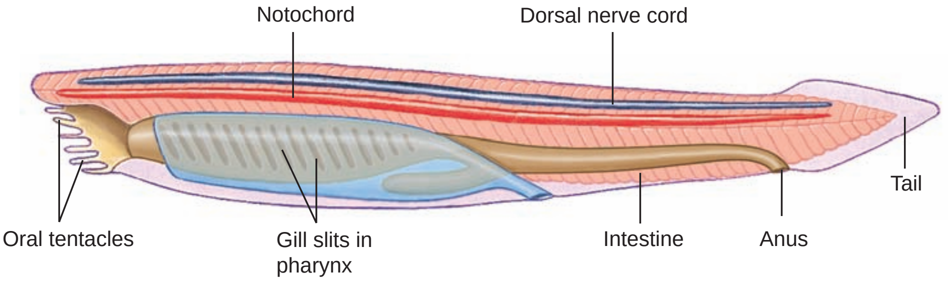

Notochord
Dorsal nerve cord
Tail
Oral tentacles
Gill slits in pharynx
Intestine
Anus

FIGURE 7.53 Though it looks like a fish, the lancelet (*Branchiostoma*) is an invertebrate because it lacks a backbone. The notochord, dorsal nerve cord, and gill slits show it is a chordate.

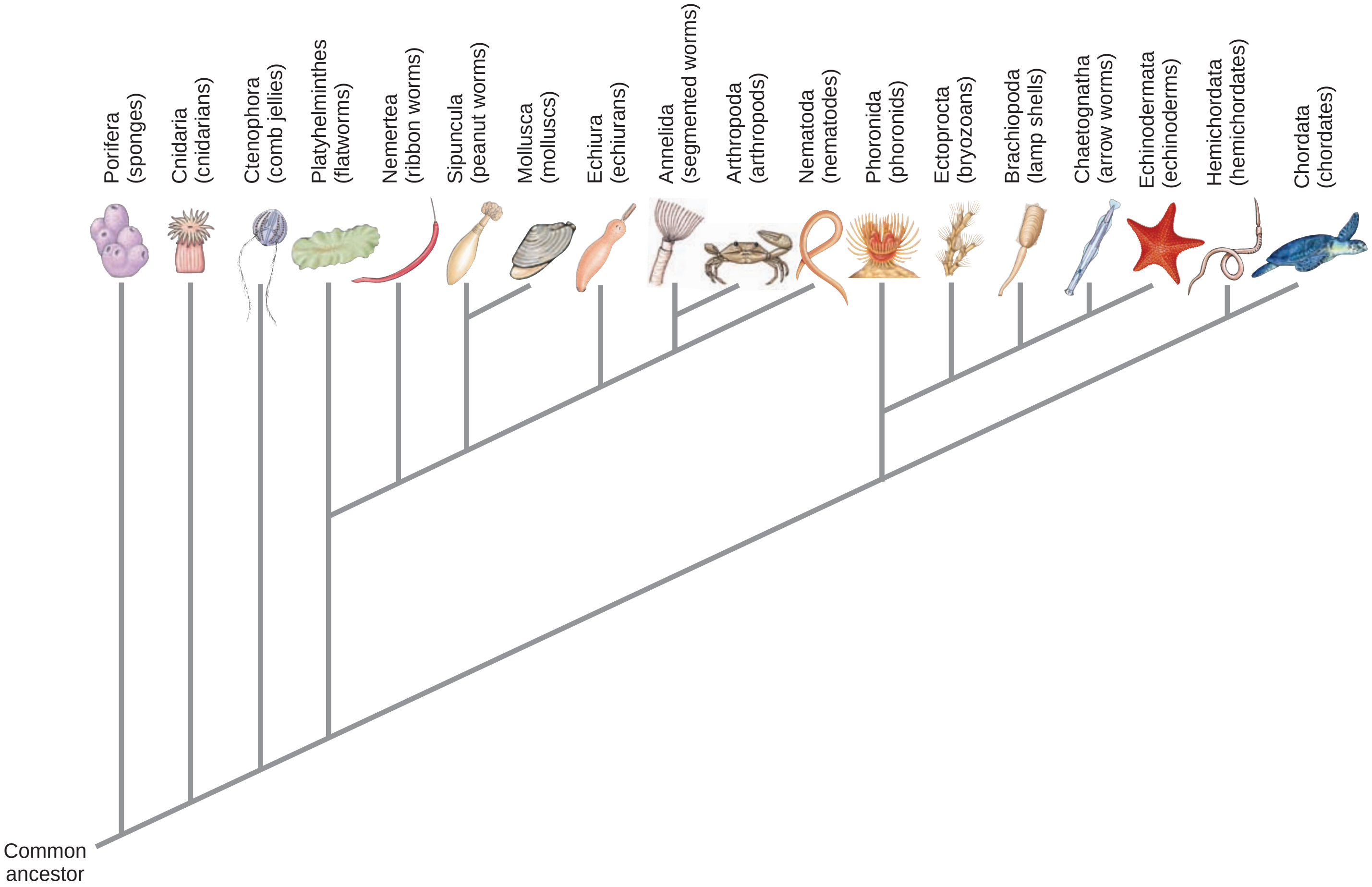
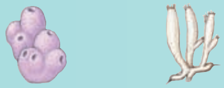
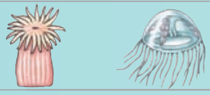
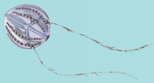
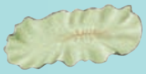
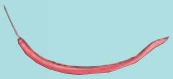
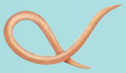
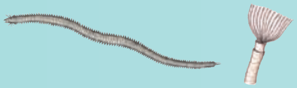
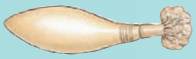
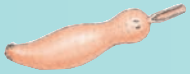
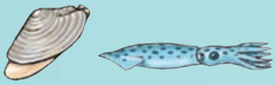
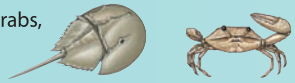
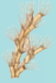
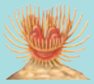
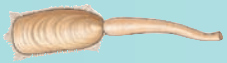
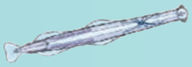
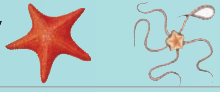
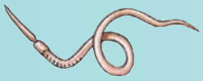
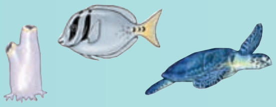

Porifera (sponges)
Cnidaria (cnidarians)
Ctenophora (comb jellies)
Platyhelminthes (flatworms)
Nemertea (ribbon worms)
Sipuncula (peanut worms)
Mollusca (molluscs)
Echiura (echiurans)
Annelida (segmented worms)
Arthropoda (arthropods)
Nematoda (nematodes)
Phoronida (phoronids)
Ectoprocta (bryozoans)
Brachiopoda (lamp shells)
Chaetognatha (arrow worms)
Echinodermata (echinoderms)
Hemichordata (hemichordates)
Chordata (chordates)
Common ancestor

FIGURE 7.54 Phylogenetic relationships among the major animal phyla. This scheme is based on many characters, including morphology, embryological development, and types of larvae. Alternative schemes based on other information have been proposed.

Lancelets

The second group of invertebrate chordates consists of 23 known species of **lancelets** (subphylum **Cephalochordata**). The body, up to 7 cm (close to 3 in) long, is laterally compressed and elongated like that of a fish (Fig. 7.53). The basic chordate characteristics are well developed throughout life. Only the lack of a backbone separates lancelets from vertebrates. Lancelets are inhabitants of soft bottoms. They are filter feeders, using the gill slits to capture and concentrate organic particles.

Table 7.1 Some of the Most Important Characteristics of the Major Animal Phyla

Phylum	Representative Groups	Distinguishing Features	General Habitat	Significance in the Marine Envionment
Porifera (sponges)	Sponges 	Collar cells (choanocytes)	Benthic	Filter feeders
Cnidaria (cnidarians)	Jellyfishes, sea anemones, corals 	Nematocysts	Benthic, pelagic	Predators, passive suspension feeders; corals are important reef builders
Ctenophora (comb jellies)	Comb jellies 	Ciliary combs, colloblasts	Mostly pelagic	Predators
Platyhelminthes (flatworms)	Turbellarians, flukes, tapeworms 	Flattened body	Mostly benthic, many parasitic	Predators, many parasitic
Nemertea (ribbon worms)	Ribbon worms 	Long proboscis	Mostly benthic	Predators
Nematoda (nematodes)	Nematodes, roundworms 	Body round in cross section	Mostly benthic, many parasitic	Many parasitic, deposit feeders
Annelida (segmented worms)	Polychaetes, oligochaetes, leeches 	Segmentation	Mostly benthic	Predators, deposit feeders, passive suspension feeders
Sipuncula (peanut worms)	Peanut worms 	Long, retractable anterior end	Benthic	Predators
Echiura (echiurans)	Echiurans 	Non-retractable proboscis	Benthic	Predators
Mollusca (molluscs)	Snails, clams, oysters, octopuses, chitons 	Foot, mantle, radula (absent in some groups)	Benthic, pelagic	Predators, grazers, filter feeders, some parasitic
Arthropoda (arthropods)	Crustaceans (crabs, shrimps), insects 	Exoskeleton, jointed legs	Benthic, pelagic, some parasitic	Predators, grazers, filter feeders, some parasitic
Ectoprocta (bryozoans)	Bryozoans 	Lophophore, colonial	Benthic	Filter feeders
Phoronida (phoronids)	Phoronids 	Lophophore, worm-like body	Benthic	Filter feeders
Brachiopoda (lamp shells)	Lamp shells 	Lophophore, clam-like shells	Benthic	Filter feeders
Chaetognatha (arrow worms)	Arrow worms 	Transparent body with fins	Filter feeders	Predators
Echinodermata (echinoderms)	Sea stars, brittle stars, sea urchins, sea cucumbers 	Tube feet, five-way radial symmetry, water vascular system	Predators	Predators, deposit feeders, passive suspension feeders
Hemichordata (hemichordates)	Acorn worms 	Dorsal, hollow nerve cord, gill slits	Mostly benthic	Deposit feeders
Chordata (chordates)	Tunicates, vertebrates (fishes, reptiles, birds, mammals) 	Dorsal, hollow nerve cord, gill slits, notochord	Benthic, pelagic	Predators, grazers, filter feeders

Level of Organization	Symmetry	Segmentation	Body Cavity	Digestive Tract	Respiratory Exchange	Circulatory System
Cellular	Asymmetrical	No	None	None	Body surface	None
Tissue	Radial	No	None	Incomplete	Body surface	None
Tissue	Radial	No	None	Incomplete	Body surface	None
Organ system	Bilateral	No	None	Incomplete or absent	Body surface	None
	Bilateral	No	Proboscis cavity	Complete	Body surface	Closed
	Bilateral	No	Pseudocoelom	Complete	Body surface	None
	Bilateral	Yes	Coelom	Complete or absent	Gills or body surface	Closed
	Bilateral	No		Complete	Body surface	None
	Bilateral	No			Body surface	Closed
	Bilateral	No			Gills	Open or closed
	Bilateral	Yes			Gills (in many crustaceans)	Open
	Bilateral	No			Body surface	None
	Bilateral	No			Body surface	Closed
	Bilateral	No			Body surface	Open
	Bilateral	No			Body surface	None
	Radial (adults) Bilateral (larvae)	No			Body surface	None
	Bilateral	Reduced			Body surface	Part closed, part open
	Bilateral	Reduced			Gills, lungs	Closed

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. If bilateral symmetry were to evolve among cnidarians, in which group or groups would you expect it to occur? Why?
2. Cephalopods, the squids, octopuses, and allies, show a much higher degree of structural and behavioral complexity than the other groups of molluscs. What factors triggered the evolution of these changes? A rich fossil record among cephalopods shows that once they were very common and even dominant in some marine environments. Now there are only about 650 living species of cephalopods, far fewer than gastropods. In the end, were cephalopods successful? What do you think happened along the way?
3. A new class of echinoderms, the sea daisies, or concentricycloids, was discovered in 1986. They are deep-water animals living on sunken wood. They are flat and round, looking very much like a small sea star without arms. They also lack a gut. Without ever having seen them, why do you think they were classified as echinoderms, not as members of a new phylum? Do you have any hypotheses as to how they feed or move around?

For Further Reading

Some of the recommended readings may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Bottjer, D. J., 2005. The early evolution of animals. *Scientific American*, vol. 293, no. 2, August, pp. 42–47. The discovery of an invertebrate fossil pushes back the origins of complex animals by at least 50 million years.

Duffy, J. E., 2003/2004. Underwater urbanites. *Natural History*, vol. 112, no. 10, December/January, pp. 40–45. Snapping, or pistol, shrimps that live in sponges have evolved complex societies similar to those of bees.

Fortey, R. A., 2004. The lifestyles of the trilobites. *American Scientist*, vol. 92, no. 5, September/October, pp. 446–453. A surprisingly high number of species of trilobites, a group of extinct arthropods, inhabited the oceans 450 million years ago.

Holland, J. S., 2007. Hawaii's unearthly worms. *National Geographic*, vol. 211, no. 2, February, pp. 118–131. Tropical Pacific worms take many shapes according to their habitats and feeding habits.

Levy, S., 2004. Crabs in space. *New Scientist*, vol. 181, no. 2438, 13 March, pp. 42–43. Cells in the blood of horseshoe crabs help space scientists detect earth microbes in space probes.

Mather, A., 2007. Eight arms, with attitude. *Natural History*, vol. 116, no. 1, February, pp. 30–36. The fascinating behavior of octopuses never fails to amaze.

McClintock, J., 2004. This is your ancestor. *Discover,* vol. 25, no. 11, November, pp. 64–69. Molecular biologists have provided additional evidence that sponges are close to the ancestors of all animals, including us.

Raffaele, P., 2005. Killers in paradise. *Smithsoman,* vol. 36, no. 3, June, pp. 80–88. Box jellyfishes are considered the most venomous organisms on the planet.

Summers, A., 2004. How a star avoids the limelight. *Natural History,* vol. 113, no. 4, May, pp. 32–33. The eyes of echinoderms, though seemingly simple, have a vital function.

Summers, A., 2004. Knockout punch. *Natural History*, vol. 113, no. 6, July/August, pp. 22–23. The claws of mantis shrimps are powerful weapons that conceal an intricate mechanism.

Summers, A., 2006. Tough as shells. *Natural History*, vol. 115, no. 5, June, pp. 28–29. Nacre, the hard material in most mollusc shells, may find its way into artificial bone and other products.

In Depth

Anderson, P., 2004. Cnidarian neurobiology: what does the future hold? *Hydrobiologia,* vol. 530, pp. 107–116.

Collins, M. A. and P. G. K. Rodhouse, 2006. Southern ocean cephalopods. *Advances in Marine Biology,* vol. 50, pp. 191–265.

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Devaraj, H. and A. Natarajan, 2006. Molecular mechanisms regulating molting in a crustacean. *European Journal of Biochemistry*, vol. 273, pp. 839–846.

Ford, A., T. Fernandes, P. Read, C. Robinson, and I. Davies, 2004. The costs of intersexuality: a crustacean perspective. *Marine Biology,* vol. 145, pp. 951–957.

Halanych, A. M., 2004. The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics*, vol. 35, pp. 229–256.

Hourdez, S. and F. Lallier, 2007. Adaptations to hypoxia in hydrothermal-vent and cold-seep invertebrates. *Reviews in Environmental Science and Biotechnology,* vol. 6, pp. 143–159.

McHugh, D., 2005. Molecular systematics of polychaetes (Annelida). *Hydrobiologia*, vol. 535, pp. 309–318.

Nielsen, C., 2005. Larval and adult brains. *Evolution & Development*, vol. 7, pp. 483–489.

Sotka, E. E., 2005. Local adaptation in host use among marine invertebrates. *Ecology Letters,* vol. 8, pp. 448–459.

Waloszek, D. and A. Maas, 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. *Evolution & Development,* vol. 7, pp. 515–527.

Manta ray (*Manta birostris*) and remoras (*Echineis naucrates*) off Key Largo, Florida.

8

CHAPTER

Marine Fishes

Fishes were the first vertebrates, appearing more than 500 million years ago. The first fishes probably evolved from an invertebrate chordate not much different from the lancelets or the tadpole larvae of sea squirts that still inhabit the oceans.

Fishes soon made their presence felt and have had a tremendous impact on the marine environment. They feed on nearly all types of marine organisms. Some of the organisms discussed in Chapters 5 through 7, from bacteria to crustaceans, use fishes as their home. Many other animals eat them.

Fishes are the most economically important marine organisms, and marine fishes are a vital source of protein for millions of people. Some are ground up for fertilizer or chicken feed. Leather, glue, vitamins, and other products are obtained from them. Many marine fishes are chased by sportfishing enthusiasts. Others are kept as pets and have brought the wonders of ocean life into many homes.

VERTEBRATES: AN INTRODUCTION

Vertebrates (subphylum **Vertebrata**) share four fundamental characteristics of the phylum Chordata with **protochordates,** the invertebrate chordates like lancelets and sea squirts. Vertebrates differ from these other chordates in having a **backbone,** also called the **vertebral column** or **spine,** which is a dorsal row of hollow skeletal elements, usually bone, called **vertebrae.** The vertebrae enclose and protect the **nerve cord,** also called the **spinal cord,** which ends in a brain that is protected by a skull made of cartilage or bone. Vertebrates also are characterized by a bilaterally symmetrical body and the presence of an endoskeleton.

> Vertebrates are chordates with a backbone that encloses a nerve cord, or spinal cord.

TYPES OF FISHES

Fishes are the oldest and structurally the simplest of all living vertebrates. They also are the most abundant vertebrates in terms of both species and individuals. About 24,000 of the at least 30,000 species of fishes are presently known to science. They make up about half of all species of vertebrates on earth. Most species of fishes, so far around 15,300, are marine. Many new

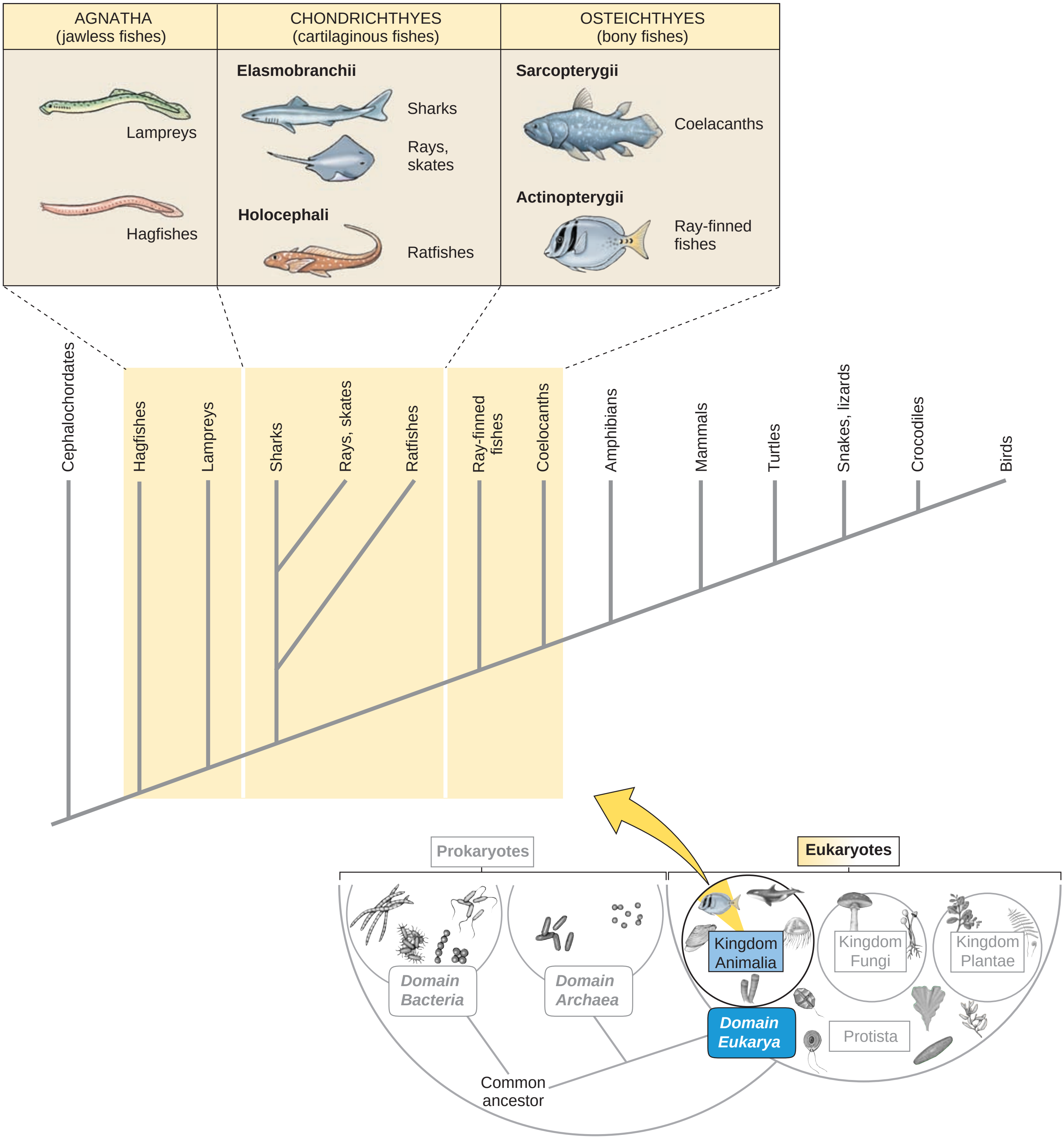

AGNATHA
(jawless fishes)
CHONDRICHTHYES
(cartilaginous fishes)
OSTEICHTHYES
(bony fishes)
Lampreys
Hagfishes
Elasmobranchii
Sharks
Rays, skates
Holocephali
Ratfishes
Sarcopterygii
Coelacanths
Actinopterygii
Ray-finned fishes
Cephalochordates
Hagfishes
Lampreys
Sharks
Rays, skates
Ratfishes
Ray-finned fishes
Coelocanths
Amphibians
Mammals
Turtles
Snakes, lizards
Crocodiles
Birds
Prokaryotes
Eukaryotes
Domain Bacteria
Domain Archaea
Kingdom Animalia
Kingdom Fungi
Kingdom Plantae
Domain Eukarya
Protista
Common ancestor

FIGURE 8.1 Classification scheme of fishes.

species are being discovered every year, so that 2,000 to 3,000 species are expected to be added to the total by 2010.

There is some disagreement as to how to classify the major groups of fishes. Three groups are traditionally recognized. One of the schemes proposed to show the relationships of these three groups with the rest of the vertebrates is given in Figure 8.1.

Jawless Fishes

The most primitive fishes living today are the **jawless fishes (Agnatha).** Because they lack jaws, they feed by suction with the aid of a round, muscular mouth and rows of teeth. The body is cylindrical and elongated like that of eels or snakes (Fig. 8.2). They lack the paired fins and scales of most fishes. Some biologists do not even consider jawless fishes to be vertebrates because they lack true vertebrae.

Hagfishes, or **slime eels** (*Myxine, Eptatretus*), are jawless fishes that feed mostly on dead or dying fishes (see Table 8.1, p. 175). They sometimes bore into their prey and eat them from the inside out. Hagfishes live in burrows they dig in muddy bottoms, mostly at moderate depths in cold waters. Only about 20 species are known. They reach a maximum length of approximately 80 cm (2.6 ft). Their skin is used in the manufacture of leather goods, but they are mostly known for attacking bait or fishes on fishing lines, nets, and traps.

Lampreys (*Petromyzon*), found in most temperate regions, are primarily freshwater fishes. They breed in rivers and lakes, but some move to the sea as adults. They attach to other fishes and suck their blood or feed on bottom invertebrates. There are an estimated 30 species of lampreys.

Hagfishes and lampreys lack jaws and are the most primitive living fishes.

Cartilaginous Fishes

The **cartilaginous fishes (Chondrichthyes)** are a fascinating and ancient group that includes the sharks, rays, skates, and ratfishes. Cartilaginous fishes have a skeleton made of **cartilage,** a material that is lighter and more flexible than bone. Though the skeleton of jawless fishes is also cartilaginous, sharks and related fishes feature some significant advances. They possess movable jaws that are usually armed with well-developed teeth (Fig. 8.3). The mouth is almost always ventral—that is, underneath the head. Another important development is the presence of paired lateral fins for efficient swimming. Cartilaginous fishes have rough, sandpaper-like skin because of the presence of tiny **placoid scales.** These consist of a pointed tip that is directed backward (see Fig. 8.8*a*) and have the same composition as teeth.

Sharks, rays, skates, and ratfishes are characterized by a cartilaginous skeleton and a rough skin covered by minute placoid scales. They also have movable jaws and paired fins.

Sharks **Sharks** are magnificently adapted for fast swimming and predatory feeding. They are often described as "mysterious," "evil," or "formidable"—evidence of our fascination with sharks.

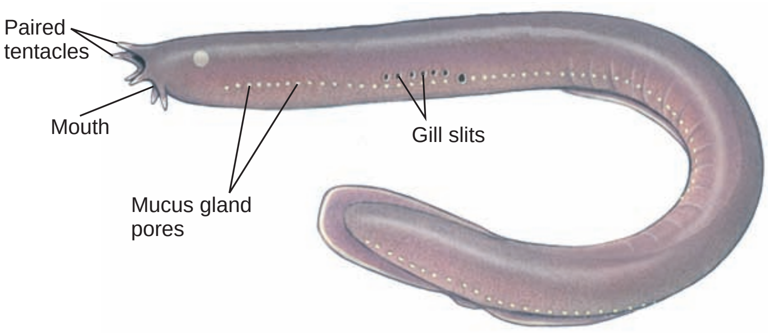


FIGURE 8.2 The Pacific hagfish (*Eptatretus stoutii*) has four pairs of sensory tentacles around the mouth and twelve pairs of gill slits. Hagfishes are also known as slime eels because of the abundant mucus produced by glands on the skin. The mucus is used by hagfishes to protect themselves while feeding with their heads buried in dead fishes and whales. Notice the absence of paired fins.

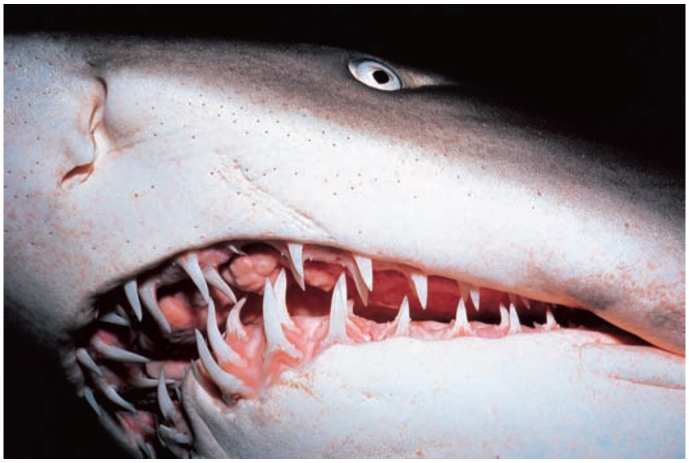


FIGURE 8.3 Shark jaws have several rows of triangular teeth. Individual teeth often have even smaller serrations, or denticles, along their edges. A tiger shark (*Galeocerdo cuvier*) may grow and discard 24,000 teeth in a 10-year period. These are the jaws of a sandtiger shark (*Carcharias taurus*). The small holes in the skin between the eye and the nostrils are the ampullae of Lorenzini (see p. 166).

Sharks are sometimes referred to as "living fossils" because many of them are similar to species that swam the seas over 100 million years ago. Their fusiform, or spindle-shaped, bodies, tapering from the rounded middle toward each end, slip easily through the water. The tail, or **caudal fin,** is well developed and powerful. The tail is usually **heterocercal,** meaning that the upper lobe is longer than the lower lobe (see Fig. 8.8*a*). The upper surface of the body typically features two **dorsal fins,**

Four basic characteristics of chordates:
1. A single, dorsal, hollow nerve cord
2. Gill, or pharyngeal, slits
3. A notochord
4. A post-anal tail

- Chapter 7, p. 145

The term "fish" is used for a single individual or for more than one individual of the same species.

The term "fishes" is used to refer to more than one species of fish.

the first of which is typically larger and nearly triangular. The paired **pectoral fins** are large and pointed in most species. Five to seven gill slits are located behind the head (see Fig. 1.17) and are present on each side of the body.

The powerful jaws of sharks have rows of numerous sharp, often triangular teeth (Fig. 8.3). The teeth are embedded in a tough, fibrous membrane that covers the jaws. A lost or broken tooth is replaced by another, which slowly shifts forward from the row behind it as if on a conveyor belt.

Not all of the nearly 350 living species of sharks conform to this body plan. Hammerhead sharks (*Sphyrna*), for example, have flattened heads with eyes and nostrils at the tip of bizarre lateral extensions (Fig. 8.4*a* and photo on p. 156). The head serves as a sort of rudder. The wide head also separates the eyes and nostrils, which improves the shark's sensory perception. The head of sawsharks (*Pristiophorus*) extends in a long, flat dorsoventrally flattened blade armed with teeth along the edges. The upper lobe of the tail is very long in the thresher sharks (*Alopias;* Fig. 8.4*k*). They use the tail to herd and stun schooling fishes, which they then eat.

The size of fully grown adults also varies. The spined pygmy shark (*Squaliolus laticaudus;* Fig. 8.4*l*) grows to no longer than 25 cm (almost 10 in). At the other extreme, the whale shark (*Rhiniodon typus;* Fig. 8.4*i* and 10.6) is the largest of all fishes. This huge animal, found in tropical waters around the world, may be as long as 18 m (60 ft), though specimens longer than 12 m (40 ft) are rare. Whale sharks pose no danger to swimmers; they are **filter feeders** that feed on plankton. Another giant, second in size only to the whale shark, is the basking shark (*Cetorhinus maximus;* Fig. 8.4*h*), also a plankton eater. There are reports of basking sharks 15 m (50 ft) long, but most do not exceed 10 m (33 ft). Another very large shark is considered the most dangerous of all—the great white shark (*Carcharodon carcharias;* Fig. 8.4*g*). Individuals may exceed 6 m (20 ft) in length.

Sharks are found throughout the oceans at practically all depths, but they are more prevalent in tropical coastal waters. Sharks are primarily marine, but a few species travel far up rivers. The bull shark (*Carcharhinus leucas;* Fig. 8.4*d*) may be permanently established in some rivers and lakes in the tropics. Several sharks are found mostly in deep water (Fig. 8.5*b*).

Shark meat is eaten around the world. Many people have tried shark without knowing because it is often illegally sold as "regular" fish or scallops. Our appetite for shark has led to disastrous overfishing. So many sharks are being caught that the number of these slow-growing and slow-reproducing fishes has sharply declined in many parts of the world. The number of whitetip sharks (*Carchirhinus longimanus*) in the Gulf of Mexico, for example, is only 1% of their number in the 1950s. Sharks are still fished for their oil, once used extensively in all kinds of products, and for their skin, which is processed into a leather called shagreen. The skin is also used as sandpaper. Much more valuable are their fins, used for soup in the Orient. Sharks are caught, their fins cut off (a practice known as shark finning), and

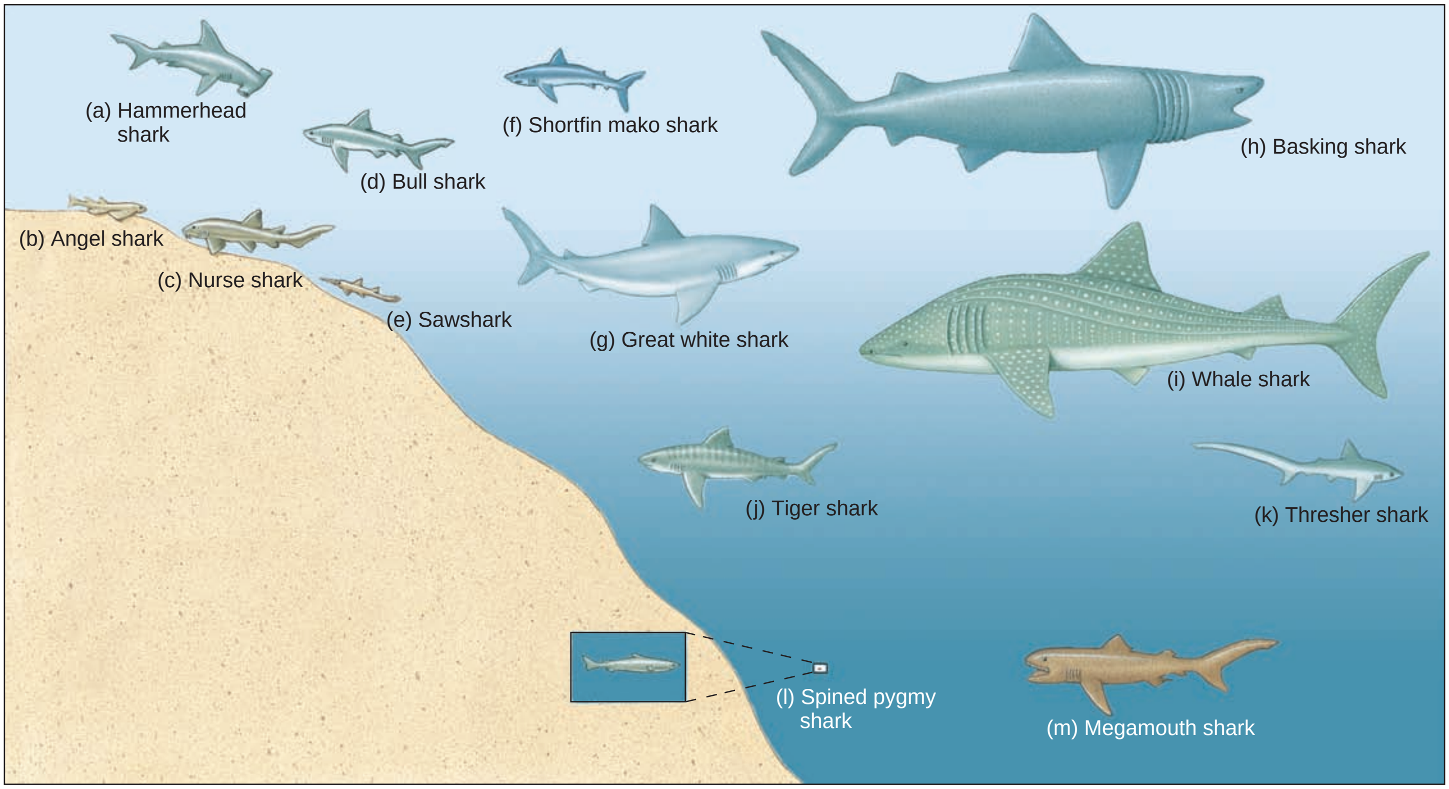


FIGURE 8.4 Sharks live practically everywhere in the ocean. Some of those mentioned in the text include (*a*) *hammerhead shark* (*Sphyrna zygaena*), (*b*) angel shark (*Squatina californica*), (*c*) nurse shark (*Ginglymostoma cirratum*), (*d*) bull shark (*Carcharhinus leucas*), (*e*) sawshark (*Pristiophorus cirratus*), (*f*) shortfin mako shark (*Isurus oxyrinchus*), (*g*) great white shark (*Carcharodon carcharias*), (*h*) basking shark (*Cetorhinus maximus*), (*i*) whale shark (*Rhiniodon typus*), (*j*) tiger shark (*Galeocerdo cuvier*), (*k*) thresher shark (*Alopias vulpinus*), (*l*) spined pygmy shark (*Squaliolus laticaudus*), and (*m*) megamouth shark (*Megachasma pelagios*).

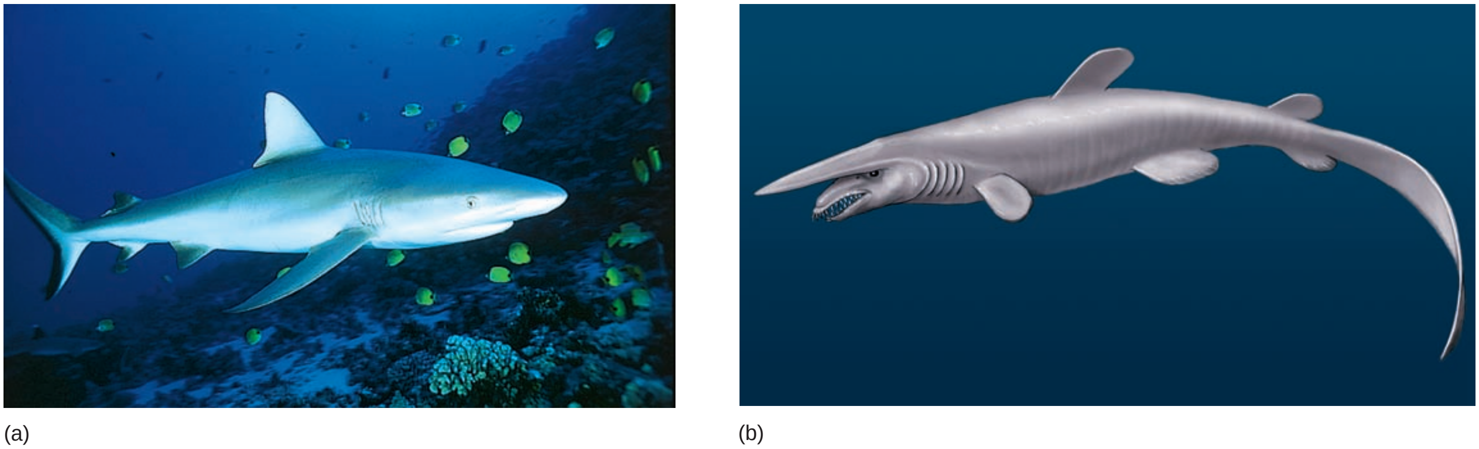


FIGURE 8.5 (*a*) The gray reef shark (*Carcharhinus amblyrhynchos*) is common in shallow waters of the tropical Pacific and Indian oceans. (*b*) The bizarre goblin shark (*Mitsukurina owstoni*) is usually found in deeper water.

the wounded animals sometimes dumped in the sea to die. The mistaken belief that shark cartilage is a "joint nutrient" that may help in the treatment of arthritis has caused even more fishing pressure. Overfishing of sharks has led to a more stringent management of shark fishing, including a ban on shark finning in the United States and other countries. There is nevertheless a booming international trade in fins. Even deep-water sharks have not escaped overfishing. Fin sales of about 1.7 million tons a year around the world translate into 73 million sharks a year, more than four times the official shark catches.

Rays and Skates The 450 to 550 species of **rays** and **skates** have dorsoventrally flattened bodies and for the most part live on the bottom (Fig. 8.6). Fishes that live on the bottom are called **demersal.** Some sharks, like angel sharks (*Squatina*) and sawsharks (*Pristiophorus*), also have flattened bodies (Fig. 8.4*b* and *e*). To complicate things, some true rays, like the guitarfishes (*Rhinobatos*), have a body that looks very much like a shark's. Only rays, skates, and related fishes, however, have their gill slits (always five pairs) on the underside of the body—that is, located ventrally (Fig. 8.6*b*)—rather than on the sides. The pectoral fins are flat and greatly expanded, looking almost like wings. They are typically fused with the head. The eyes are usually on top of the head.

The tropical sawfishes (*Pristis*) look very much like sawsharks but have ventral gill slits and are therefore grouped with the rays and skates. They feed by swimming through schools of fish and swinging their blades back and forth to disable their prey. They are known to grow up to 11 m (36 ft) long.

Many species of **stingrays** (Fig. 8.6*a*) and their relatives—the eagle, bat, and cow-nosed rays—have a whip-like tail usually equipped with stinging spines at the base for defense. Poison glands produce venom that can cause serious wounds to anyone who steps or falls on them. Abdominal wounds from stingrays, which often occur when handling rays caught in nets, may result in death. Many stingrays cover themselves with sand, becoming nearly invisible. They feed on clams, crabs, small fishes, and other

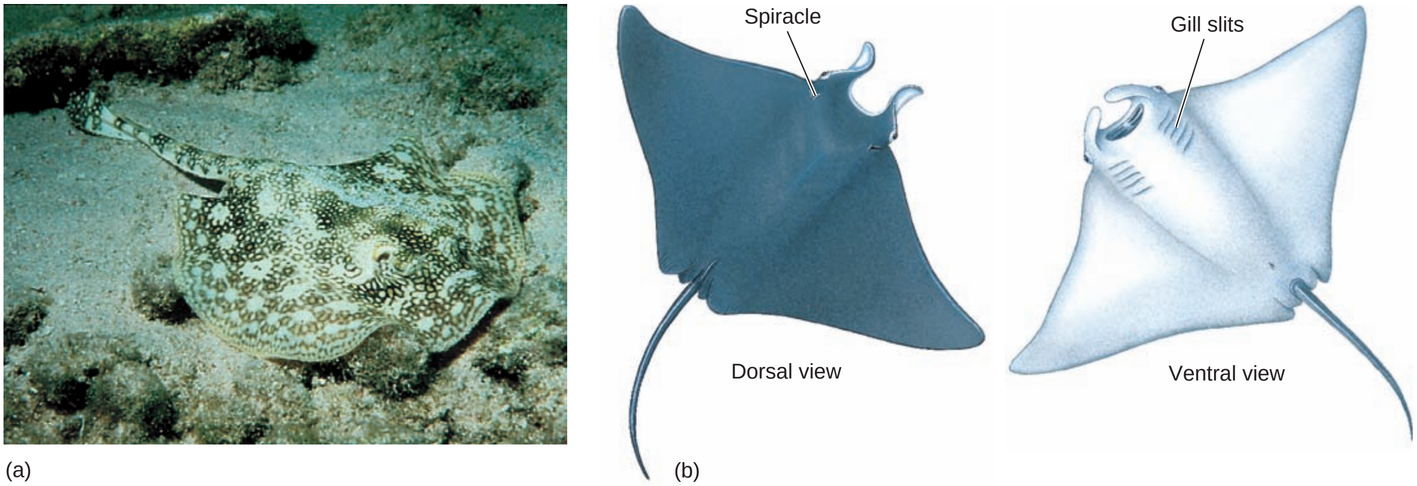


FIGURE 8.6 Rays and skates have a flattened body and ventral gill slits. Examples are (*a*) the yellow stingray (*Urolophus jamaicensis*) and (*b*) the manta ray (*Manta birostris*).

Shark!

The scalloped hammerhead shark (*Sphyrna lewini*) is not considered dangerous to humans.

Most sharks are harmless—at least to humans. Nevertheless, 25 species of sharks are known to have attacked humans, and at least 12 more are suspected of doing so. Three are particularly dangerous: the great white, tiger, and bull sharks (see Fig. 8.4). The number of unprovoked attacks around the world was 61 (4 fatal) in 2005, 62 (4 fatal) in 2006. The annual average for the 1990s was 54 (12.7 fatal), 64.8 (5.5 fatal) in the years since 2000. Even when more tourists are visiting less spoiled areas, shark attacks are rare. The chances of being attacked by a shark are lower than those of being hit by lightning.

Many shark attacks, however, have been documented over the years: a diver in Southern California was last seen protruding from the mouth of a shark, parts of arms and legs were found in the stomach of a tiger shark caught after a man had been mortally wounded in Australia, and a series of attacks by tiger sharks have occurred in Hawai‘i. One of the authors knew a young man whose promising life ended horribly in the jaws of a tiger shark off Western Samoa.

World War II exposed the crews of torpedoed ships and downed airplanes to shark attacks. Many grim stories about bleeding bodies surrounded by sharks began to spread. They prompted research on the aggressive behavior of sharks and the circumstances leading to shark attacks.

Great white sharks typically inflict a massive wound on their prey (such as seals and sea lions) and then release it. The sharks wait until the bleeding prey is too weak to resist, then move in for the kill. White shark attacks on humans wearing wet suits may be cases of mistaken identity. Sometimes people are able to escape when sharks release them after the first bite. It has been discovered that before attacking, sharks may display distinctive aggressive behaviors—pointing downward of the pectoral fins, pointing upward of the nose with back hunched, or the shivering of the body. Displaying sharks may attack if someone approaches.

So far there is no absolutely guaranteed shark repellent. Copper acetate was used during World War II as a repellent but was eventually found to be ineffective. A black dye was used, but this helped only by obscuring the shark's vision. A chemical repellent is now available in the United States. Chain mail suits offer effective protection from sharks but are too expensive and cumbersome for widespread use. For someone like a downed flyer or shipwrecked sailor, perhaps the best protection is a black plastic bag large enough to float inside.

How can you decrease the risk of an attack? First, do not swim, dive, or surf in an area known to be frequented by dangerous sharks. Seal and sea lion colonies and coastal garbage dumps attract them. Blood, urine, and feces also attract sharks. Avoid murky water. Many sharks are more active at night, so avoid night swims. Sharks should not be provoked in any way. Even resting nurse sharks can turn and bite. Leave the water if fish suddenly appear in large numbers and behave erratically, which may be an indication that sharks are around. If you see a large shark, get out of the water with as little splashing as possible. If attacked, hit the shark's nose or gills with any object on hand, a spear or camera, but not with your bare hands! Do not panic.

Actually, we threaten the survival of sharks more than they threaten us. They reproduce slowly, and their numbers are being depleted by overfishing. This attitude toward sharks may be shortsighted, because they play an important role in marine communities. Overfishing of sharks in Caribbean coral reefs has triggered an increase in the number of groupers and other small predators, which prey on parrot fishes and other algal feeders. Algae then thrive, growing over and killing reef-building corals. Some catch shark only for the shark's fins or jaws. Others practice shark hunting for sport, leaving the meat to waste. A magnificent predator, the shark may soon be exterminated by humans, the fiercest predators of all.

small animals that live in sediment. Stingrays have been known to damage valuable shellfish beds. They expose their food by excavating sediment with their pectoral fins. Their teeth are modified into grinding plates that crush their prey.

Electric rays (*Torpedo*) have special organs that produce electricity on each side of the head. They can deliver shocks of up to 200 volts that stun the fishes they eat and discourage predators. The ancient Greeks and Romans used the shocks of electric rays to cure headaches and other ailments, the original shock treatment.

Not all rays spend their lives on the bottom. Eagle rays (*Aetobatus*) and the spectacular manta and devil rays (*Manta, Mobula*) "fly" through the water, using their pectoral fins like wings. Eagle rays return to the bottom to feed. Mantas feed in midwater on plankton. Both have been observed leaping out of the water. The manta ray (*Manta birostris;* Fig. 8.6*b* and photo on p. 151) grows into a majestic giant. One individual was found to be almost 7 m (23 ft) wide.

Skates (*Raja*) are similar to rays in appearance and feeding habits, but they lack a whip-like tail and stinging spines. Some have electric organs. Skates lay egg cases, whereas rays give birth to live young. Skates can be extremely abundant, and the larger species are fished for food in some parts of the world.

Ratfishes About 30 species of strange-looking, mostly deep-water, cartilaginous fishes are grouped separately because of their unique features. The **ratfishes,** or **chimaeras** (Fig. 8.7), for instance, have only one pair of gill slits covered by a flap of skin. Some have a long, rat-like tail. They feed on bottom-dwelling crustaceans and molluscs.

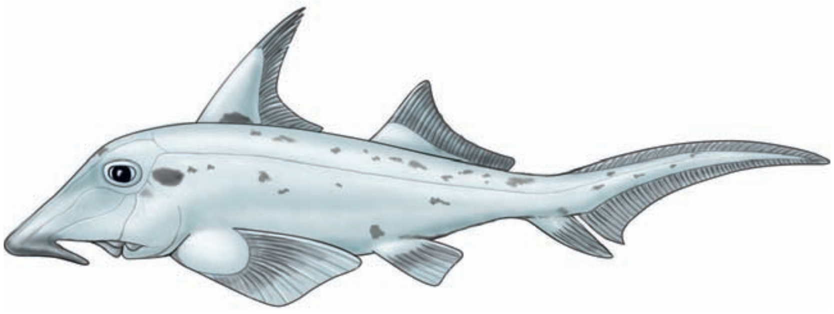


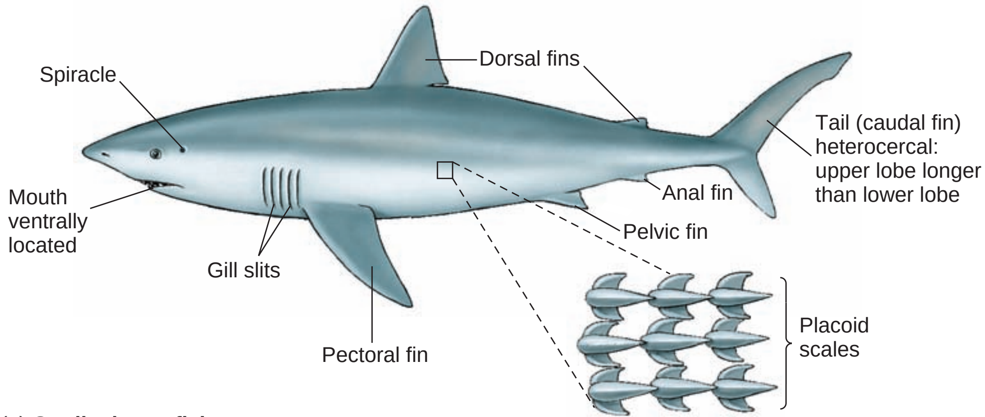
FIGURE 8.7 The elephant fish (*Callorhinchus*), an example of a ratfish, or chimaera. The elephant fish, which is caught commercially for food in the Southern Hemisphere, receives its name because of a snout that hangs down like an elephant's trunk.

Bony Fishes

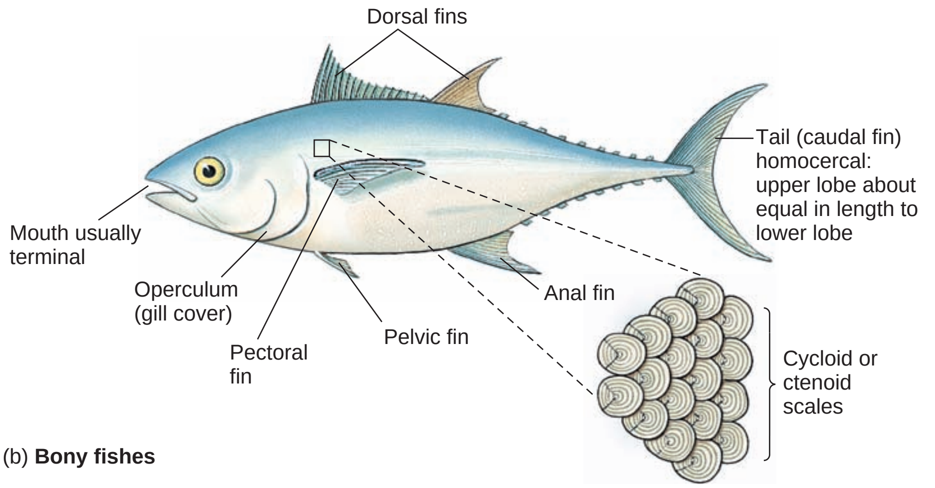
The great majority of fishes are **bony fishes (Osteichthyes).** As the name implies, they have a skeleton made at least partially of bone. There are approximately 23,000 species of bony fishes—about 96% of all fishes and almost half of all vertebrates. Between 75 and 100 new species are described every year. A little more than half of all bony fishes live in the ocean, where they are by far the dominant vertebrates.

The composition of the skeleton is not the only distinguishing feature of bony fishes. In contrast to the tiny, pointed placoid scales of cartilaginous fishes, bony fishes usually have **cycloid** or **ctenoid scales,** which are thin, flexible, and overlapping (Fig. 8.8*b*). Cycloid scales are smooth, whereas ctenoid scales have many tiny spines along their exposed borders. The scales are made of bone and are covered by a thin layer of skin (see Fig. 8.19) as well as protective mucus. Some bony fishes, however, lack scales altogether. Another characteristic of bony fishes is the presence of an **operculum,** or **gill cover,** a flap of bony plates and tissue that protects the gills.

The upper and lower lobes of the tail, the caudal fin, are generally the same size, or **homocercal** (Fig. 8.8*b*). The fins of bony fishes generally consist of thin membranes that are supported by bony spines, or **fin rays,** in contrast to the stiff, fleshy fins of cartilaginous fishes. Fin rays may consist of rigid spines that act as rudders or are used for protection. Some are flexible and used for propulsion and added maneuverability.


Dorsal fins
Spiracle
Tail (caudal fin) heterocercal: upper lobe longer than lower lobe
Mouth ventrally located
Anal fin
Pelvic fin
Gill slits
Placoid scales
Pectoral fin

(a) **Cartilaginous fishes**


Dorsal fins
Tail (caudal fin) homocercal: upper lobe about equal in length to lower lobe
Mouth usually terminal
Operculum (gill cover)
Anal fin
Pelvic fin
Pectoral fin
Cycloid or ctenoid scales

(b) **Bony fishes**

FIGURE 8.8 The most important external differences between (*a*) cartilaginous and (*b*) bony fishes. Also see Figure 8.12.

Whereas cartilaginous fishes have a ventral mouth, the mouth of most bony fishes is terminal—that is, located at the anterior end. Bony fishes have jaws with much more freedom of movement than those of sharks. The jaws of bony fishes are said to be protrusible because they can be projected outward from the mouth. The teeth are generally attached to the jawbones. Though they are usually replaced, the new teeth do not move forward in rows as do those in sharks.

Another important characteristic is the presence in many bony fishes of a **swim bladder,** a gas-filled sac just above the stomach and intestine (see Fig. 8.12*b*). It allows the fish to adjust its buoyancy to keep from sinking or rising (see "Increased Buoyancy," p. 338). This is a significant development that compensates for the relatively heavy bony skeleton.

Bony fishes are the largest group of living vertebrates. In addition to their bony skeleton, they typically have gills covered by opercula, highly maneuverable fins, protrusible jaws, and usually a swim bladder.

As we shall see in the section "Biology of Fishes," bony fishes are extraordinarily diverse in shape, size, color, feeding habits, reproductive patterns, and behavior. They have adapted to nearly every type of marine environment. All land vertebrates evolved from early bony fishes.

BIOLOGY OF FISHES

Discovering how fishes, cartilaginous and bony alike, have adapted to their environment so successfully is one of the objectives of **ichthyology,** the scientific study of fishes.

Body Shape

The body shape of a fish is directly related to its lifestyle. Fast swimmers like sharks, tunas (*Thunnus, Euthynnus*), mackerels (*Scomber, Scomberomorus*), and marlins (*Makaira*) have a streamlined body shape that helps them move through the water (Figs. 8.8 and 8.9*a;* also see "Swimming Machines," p. 345). Laterally compressed bodies are good for leisurely swimming around coral reefs, kelp beds, or rocky reefs but are still efficient enough to allow for bursts of speed to escape from enemies or capture food. This body form is seen in many inshore fishes like snappers (*Lutjanus*), wrasses (*Labroides, Thalassoma*), damselfishes (*Amphiprion, omacentrus*), and butterflyfishes (*Chaetodon;* see Fig. 8.28). Many demersal fishes, like rays, skates, and sea moths (*Pegasus;* Fig. 8.9*b*), are dorsoventrally flattened. Flatfishes such as flounders (*Platichthys*), soles (*Solea*), and halibuts (*Hippoglossus*) are flat and beautifully adapted to live on the bottom, but their bodies are actually laterally compressed (Fig. 8.9*c*). They lie on one side, with both eyes on top. They begin life with one eye on each side like other fishes, but as they develop one eye migrates up to lie next to the other one. Distinctly elongated bodies are characteristic of moray eels (*Gymnothorax*), trumpetfishes (*Aulostomus*), and pipefishes (*Sygnathus*), among others. Eel-like fishes often live in narrow spaces in rocks or coral reefs, or among vegetation (Fig. 8.9*d–f*). Many bony fishes, like seahorses (*Hippocampus;* Fig. 8.9*g*) depart from these generalized shapes. Trunkfishes (*Ostracion*) have truncate, or relatively short, bodies (Fig. 8.9*h*).

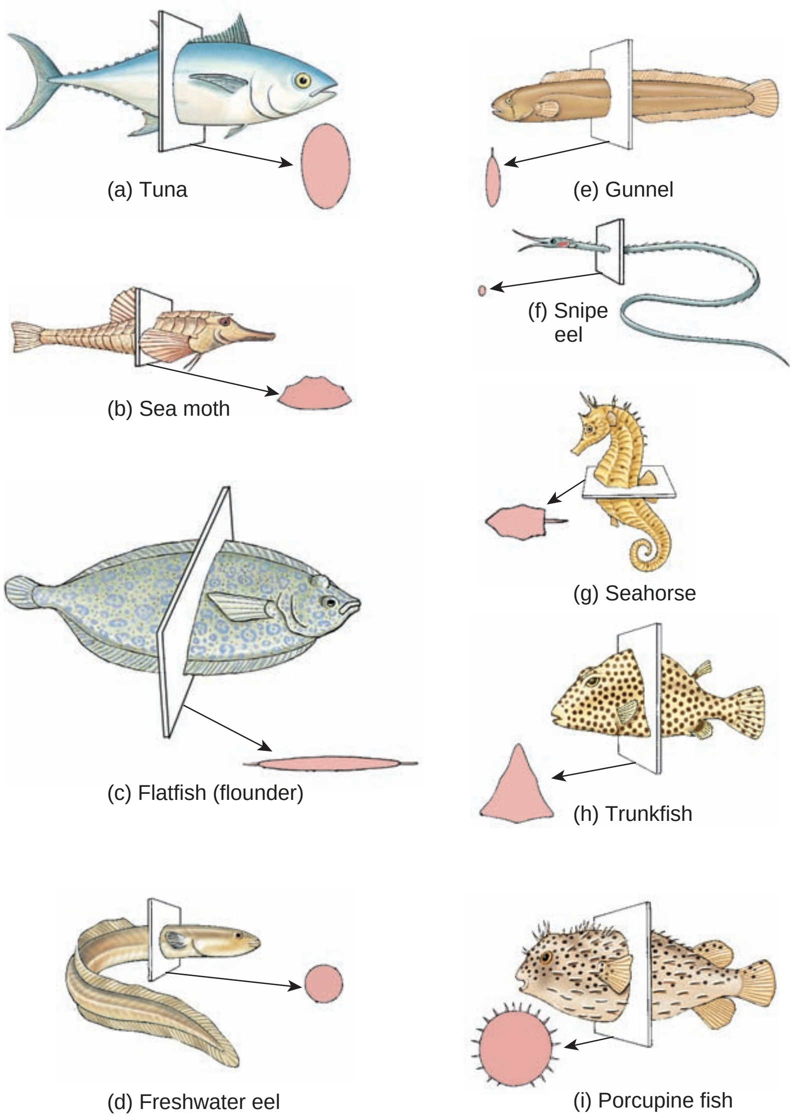


FIGURE 8.9 Body shape among bony fishes varies as an adaptation to habitat. It is streamlined for fast swimming in tunas (*Thunnus; a*); dorsoventrally flattened in bottom-dwellers such as the sea moth (*Pegasus; b*); or laterally flattened in bottom-dwellers such as the flounder (*Platichthys; c*). Fishes living among vegetation or rocks have eel-like bodies, as in the freshwater eel (*Anguilla; d*); ribbon-shaped, as in the gunnel (*Pholis; e*); or thread-like, as in the snipe eel (*Nemichthys; f*). Slow swimmers feature bodies that are elongated on a vertical plane, as in the seahorse (*Hippocampus; g*); triangular, as in the trunkfish (*Ostracion; h*); or round, as in the porcupine fish (*Diodon; i*).

Body shapes can be especially useful for camouflage. For example, some pipefishes live among the eelgrass they resemble. The long, thin trumpetfishes often hang vertically among gorgonian corals or tube-like sponges, or even sneak behind other fish when approaching prey. An irregular shape is often an excellent means of concealment. Bottom fishes such as blennies (*Blennius*) and sculpins (*Oligocottus*) have their outline broken up with irregular growths, particularly on the head, that resemble seaweeds. The body of the stonefish (*Synanceia verrucosa;* Fig. 8.10*a*) resembles a rock so closely that it is almost invisible to both potential prey and humans. Unfortunately for humans, this shallow-water fish from the tropical Pacific and Indian oceans possesses the most potent venom known in fishes. Stepping on a stonefish is excruciatingly painful and potentially fatal.

Coloration

Some bony fishes use color for camouflage, but others, particularly those living in the tropics, are among the most brightly colored animals in the sea. The colored pigments in bony fishes are mostly found in special cells in the skin called **chromatophores.** These cells are irregular in shape and have branches radiating from the center. The amazing variety of colors and hues observed

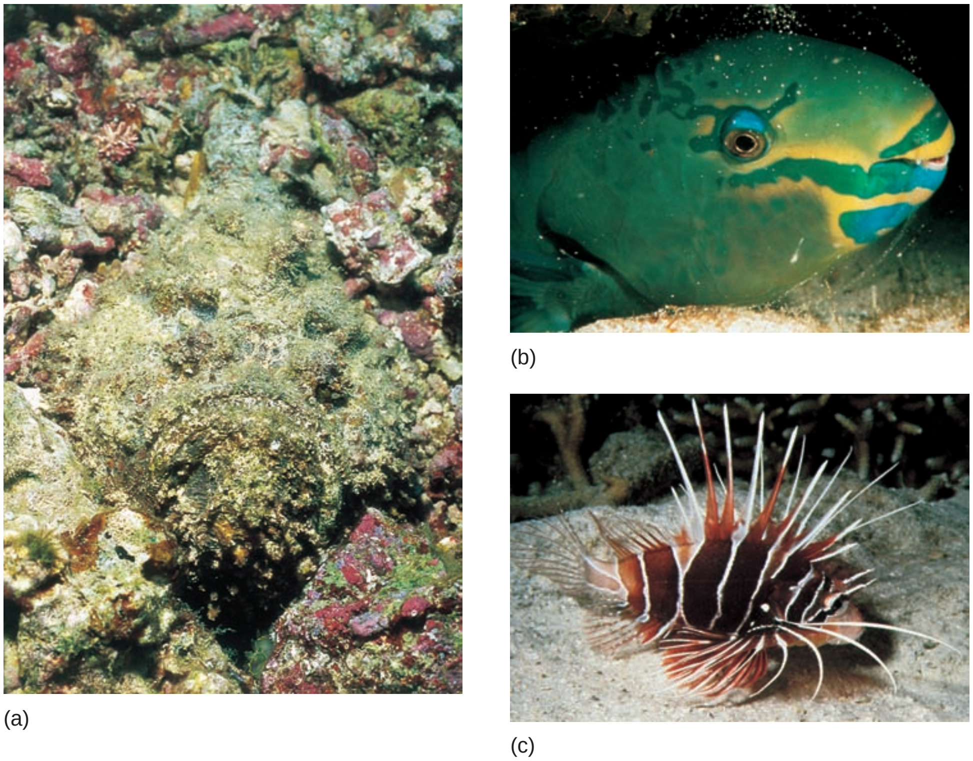


FIGURE 8.10 The variety of forms and habits among marine bony fishes is spectacular. (*a*) The stonefish (*Synanceia verrucosa*) does look like a stone, thus concealing its deadly venom. (*b*) The queen parrotfish (*Scarus vetula*) and other parrotfishes, so called because of their beak-like mouths, sleep at night by secreting a loose mucus envelope that surrounds the body. (*c*) A colorful bar-tailed lionfish (*Pterois radiata*) advertises spines that contain a powerful venom that sometimes kills humans.

among marine fishes results from combinations of chromatophores with varying amounts of different pigments. Many fishes can rapidly change color by contracting and expanding the pigment in the chromatophores. Fishes may also have **structural colors** that result when a special surface reflects only certain colors of light. Most structural colors in fishes are the consequence of crystals that act as tiny mirrors. The crystals are contained in special chromatophores called **iridophores.** The iridescent, shiny quality of many fishes is produced by structural colors in combination with pigments (Fig. 8.10*b*).

Colors can tell us a lot about fishes. Some change color with their mood or reproductive condition. They may also use color to advertise the fact that they are dangerous, are poisonous, or taste bad—a phenomenon known as **warning coloration** (Fig. 8.10*c*). **Cryptic coloration,** blending with the environment to deceive predators or prey, is a common adaptation (Fig. 8.10*a*). Flatfishes and some blennies, sculpins, rockfishes (*Sebastes*), and others can change color to match their surroundings. Another use of color is **disruptive coloration,** the presence of color stripes, bars, or spots that help break up the outline of a fish. These and other uses of color are especially common among coral reef fishes (see Figs. 8.28 and 14.30).

Open-water fishes and many shallow-water predators, on the other hand, are rarely as colorful. Most of them have silver or white bellies in sharp contrast to dark backs (see Fig. 8.8). This distinctive color pattern, known as **countershading,** is a form of disguise in open water (see "Coloration and Camouflage," p. 340). Deep-water fishes also use color for concealment. They tend to be black or red, both of which are hard to see in the ocean depths (see "Coloration and Body Shape," p. 364).

Locomotion

Swimming is obviously a major part of the life of fishes. Fishes swim to obtain food, escape from predators, and find mates. Many cartilaginous and some bony fishes must also swim to flush their gills with water to obtain oxygen.

Most fishes swim with a rhythmic side-to-side motion of the body or tail. **S**-shaped waves of contractions moving from head to tail push against the water and force the body forward. Variations on this theme are illustrated in Figure 8.11.

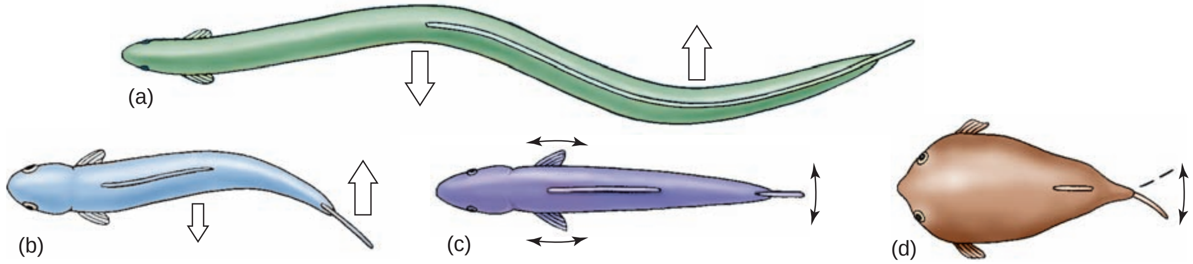


FIGURE 8.11 Locomotion in marine fishes. (*a*) Eels and other elongate fishes swim by undulating their body in lateral waves that travel from head to tail. (*b*) Fast fishes with shorter bodies—like tunas, snappers, and jacks—swim by flexing mainly the caudal (tail) portion of the body. (*c*) Surgeonfishes, parrotfishes, and others swim mainly by moving only the fins—that is, the caudal (tail), pectoral, anal, and/or dorsal fins. (*d*) Trunkfishes and porcupine fishes swim slowly by moving the base of the tail while the rest of the heavy body remains immobile.

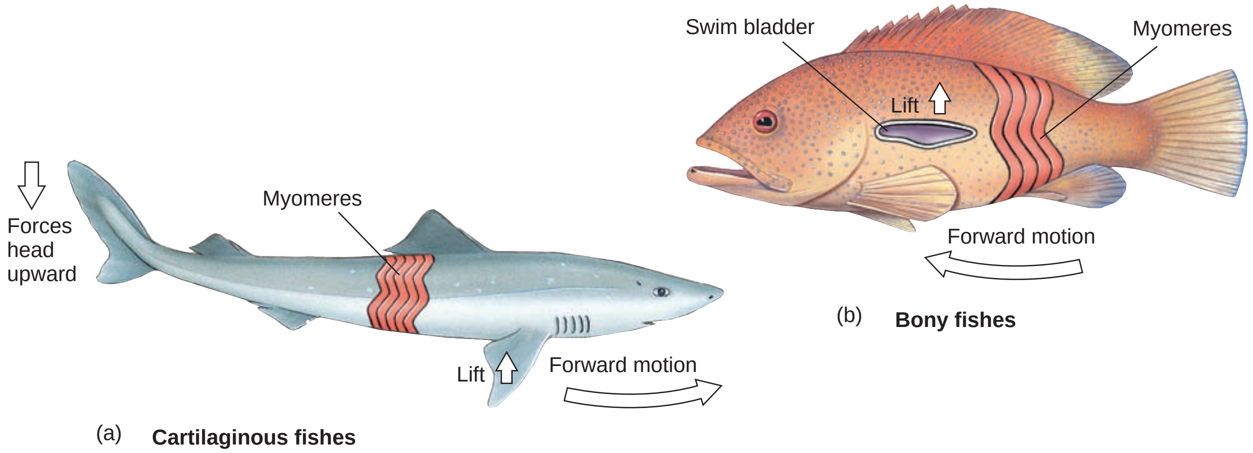


FIGURE 8.12 Cartilaginous and bony fishes use different adaptations to maintain their position in the water. (*a*) Sharks use their fins for lift. (*b*) Many bony fishes have evolved a gas-filled swim bladder to compensate for their heavier bony skeleton. This frees their fins for maneuverability, resulting in a much greater diversity of swimming styles (see Fig. 8.11).

The rhythmic contractions are produced by bands of muscle called **myomeres,** which run along the sides of the body (Fig. 8.12). The distinctive bands of muscle are easily seen in fish fillets. Myomeres are attached to the backbone for support. Muscles make up a large percentage of the body weight of a fish—as much as 75% in tunas and other active swimmers.

Sharks tend to sink because they lack the buoyant swim bladder of most bony fishes. To compensate, they have large, stiff pectoral fins that provide lift somewhat like the wings of a plane (Fig. 8.12*a*). The longer upper lobe of the tail tends to tilt the body upward, also generating some lift. The large amount of oil in the huge liver also provides buoyancy because it is less dense than water. In rays and skates the tail is greatly reduced and the pectoral fins are the main source of both thrust and lift, as in bird wings.

Because most bony fishes have a swim bladder, they do not have to rely on their pectoral fins to provide lift. The pectorals are thus free to serve other purposes. This gives bony fishes great maneuverability. Some can hover in the water or even swim backward, things that sharks cannot do. The other fins of bony fishes also help provide maneuverability. The dorsal and **anal fins** (see Fig. 8.8*b*) are used as rudders, at least part of the time, to steer and provide stability. The paired **pelvic fins** (see Fig. 8.8*b*) also help the fish turn, balance, and "brake."

The flexibility of their fins has allowed many bony fishes to depart from the standard undulating style of swimming. Some open-water bony fishes, such as tunas, emphasize sheer speed (see "Swimming Machines," p. 345). Many fishes, particularly those living around coral reefs, rocks, or kelp beds, swim mainly by moving their fins rather than their bodies, especially for the precise movements needed in feeding. Their tails are used almost solely as rudders. Wrasses, surgeonfishes (*Acanthurus*), and parrotfishes (*Scarus, Sparisoma*), which all live on coral reefs, and the California sheephead (*Semicossyphus pulcher*), common in kelp beds, swim mainly with their pectoral fins. Triggerfishes (*Balistes*) undulate their dorsal and anal fins to swim. This style is perfect for hovering over the bottom while hunting for crabs and sea urchins. Flying fishes (*Cypselurus*) have greatly expanded pectoral fins, which they use to glide through the air (see Fig. 15.21). A large variety of bottom fishes (gobies, sculpins, and many others) crawl or rest on the bottom on their pectoral and/or pelvic fins (see Fig. 8.9*b*). Clingfishes (*Gobiesox*) are small fishes that have their pelvic fins modified into part of a sucker that allows them to attach to rocks. Remoras, or sharksuckers (*Echeneis*), attach to sharks, whales, turtles, and many types of large fishes, using a large sucker on top of their heads (see photo on p. 151). This sucker is derived from part of the dorsal fin.

Fishes usually swim with sideways undulations of the body and tail. The pectoral fins and tail of sharks have an important role in buoyancy control. The fins and tail of bony fishes are generally not used to control buoyancy and instead have become highly maneuverable and important in swimming.

Feeding

Most sharks are carnivores, but in contrast to typical carnivores, which capture smaller prey, some sharks feed by taking bites from prey larger than themselves. For this they use their formidable jaws coupled with shaking of the head. A few sharks are not particular; almost anything can be found in a shark's stomach. A tiger shark (see Fig. 8.4*j*) that was caught off South Africa was found to contain the front half of a crocodile, the hind leg of a sheep, three gulls, and two cans of peas. Nurse sharks feed mostly on bottom invertebrates, including lobsters and sea urchins. Some deep-water sharks subsist mainly on squids. Cookie-cutter sharks (*Isistius*) are small, deep-water sharks that attack larger fishes and dolphins and cut out chunks of flesh with their razor-sharp teeth and sucking lips. Even the rubber sonar domes of nuclear submarines have not escaped their bites. It has been suggested that these sharks use bioluminescence to imitate squids in order to lure their prey.

Several species of cartilaginous fishes are filter feeders: the whale shark, the basking shark, the manta and devil rays, and the megamouth shark (*Megachasma pelagios;* see Fig. 8.4*m*), a gigantic deep-water shark discovered off the Hawaiian Islands in 1976 and soon after in Southern California and several other locations around the world. Like other filter-feeding fishes, basking sharks filter the water with their **gill rakers,** slender projections on the inner surface of the **gill arches** (see Fig. 8.17*b*). Whale sharks have filter plates made of modified placoid scales. The large mouths of the three filter-feeding sharks have many small teeth and, excluding the megamouth, very long gill slits. The width of the spaces between the gill rakers or filter plates determines the size of the food captured. Water is strained through the gill rakers, and the shark swallows the food that is left behind. Whale sharks feed in warm water on small schooling fishes, squids, and planktonic crustaceans. Basking sharks, which live in colder water, feed on plankton by opening their mouths and slowly swimming through the water (see Fig. 8.4*h*).

Mantas feed on plankton and small fishes, filtering them from the water with their gill rakers. Two fleshy, horn-shaped projections on the sides of the manta's mouth help channel food into the cavernous mouth (see Fig. 8.6*b* and the photo on p. 151).

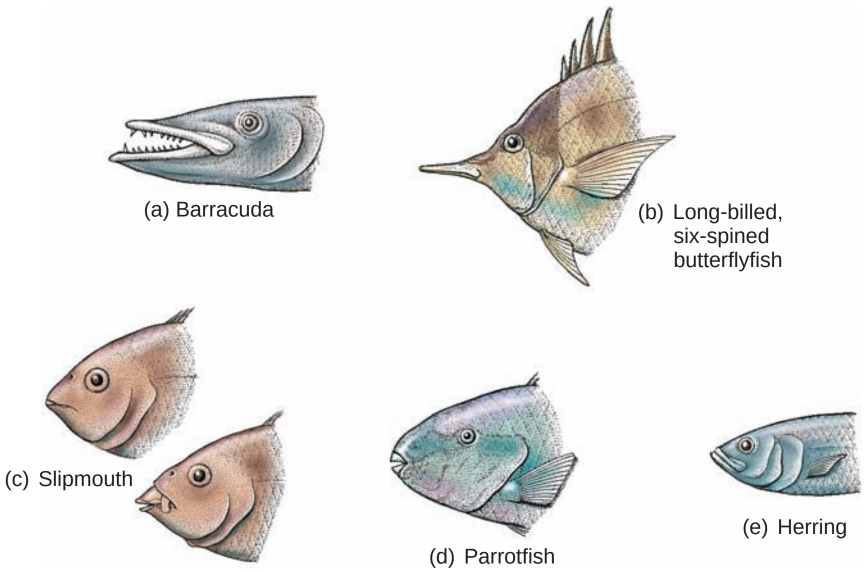


FIGURE 8.13 The shape of the mouth of bony fishes tells much about their diets. (*a*) The barracuda (*Sphyraena*) uses its large mouth to tear off chunks of prey. Most bony fishes, however, swallow their prey whole. (*b*) Many butterflyfishes (*Chaetodon*) use a long snout and small mouth to feed on very small prey. (*c*) The extremely protrusible mouth of the slipmouth (*Leiognathus*) is used for feeding on relatively small prey. (*d*) Parrotfishes (*Scarus*) use their beak-like mouth to graze on small algae and coral (see Fig. 8.10*b*). (*e*) Herrings (*Clupea*) and other filter feeders typically have large mouths.

Bony fishes are very diverse in the ways they feed. Their protrusible jaws allow them much more flexibility in feeding habits than sharks and rays have. Most bony fishes are carnivores; most groups of animals in the ocean are subject to being eaten by some bony fish. Bony fishes capture their prey from sediments, the water column, the surface of rocks, or other organisms, including other fishes, or combinations of these. Some chase their prey; others sit and wait.

Carnivorous bony fishes typically have well-developed teeth for catching, grasping, and holding their prey (Fig. 8.13*a*), which is usually swallowed whole. The roof of the mouth, gill rakers, and pharynx may also have teeth to help hold the prey. Deep-water fishes often have huge mouths and teeth (see Fig. 16.10), and a few capture and swallow prey larger than themselves.

Unusual food preferences have evolved in fishes. Some prefer sponges, infrequently touched by other carnivores. Others prefer sea urchins, sea squirts, or other seemingly tough-to-eat food items. Reef corals, skeleton and all, are eaten by several types of fishes including some butterflyfishes and parrotfishes, though only the living tissue is digested (Figs. 8.13*b* and 8.28). Many species, however, are non-specialists and capture a wide variety of prey. Some feed on small invertebrates and dead animal material from the bottom. These bottom feeders have a downward-oriented mouth adapted to suck food from the bottom. Frogfishes (*Antennarius*) and anglerfishes (*Gigantactis*; see Fig. 16.21) use a modified spine on the head to lure small fishes.

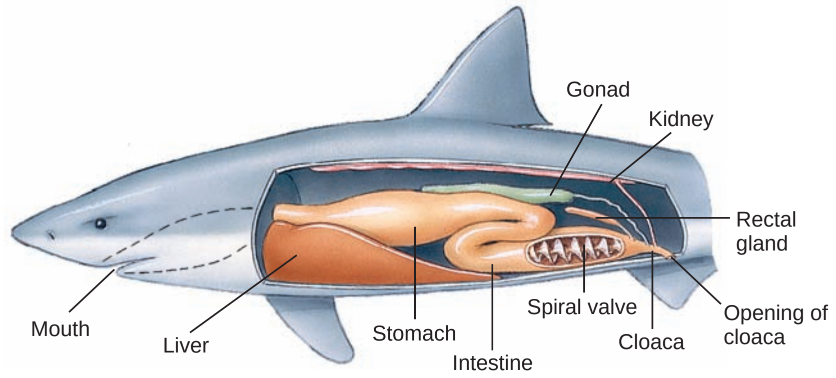
Fishes that feed primarily on seaweeds and plants are known as **grazers.** Parrotfishes, for example, graze on small algae growing on hard surfaces. Their front teeth are fused to form a beak-like structure (Fig. 8.13*d*). Some species use the beak to scrape off bits of live coral.

Fishes such as herrings (*Clupea*), sardines (*Sardinops*), anchovies (*Engraulis*), and menhadens (*Brevoortia*) filter plankton with their gill rakers. They typically strain their food by swimming with their large mouths (Fig. 8.13*e*) open. These plankton feeders are small, in contrast to the huge plankton-feeding sharks. They usually occur in large, often immense, schools. Plankton feeders are the most abundant fishes in the ocean, and they are an important food source for many types of carnivores. They also account for a large share of the world's fish catch (see "Major Food Species," p. 383).

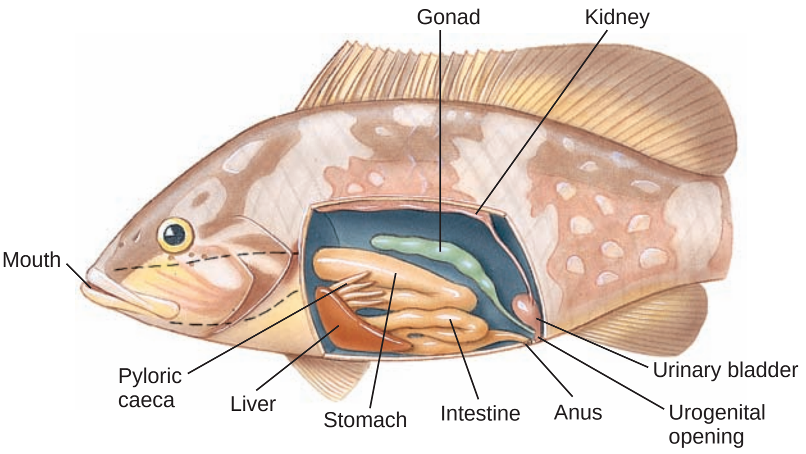
Digestion

After being swallowed, food passes through the pharynx and a short tube called the **esophagus** into the **stomach** (Fig. 8.14). The stomach is where the process of digestion usually begins. It is typically **J**-curved or elongated but may be modified into a grinding structure or even lost altogether. The food passes from the stomach into the **intestine.** In most bony fishes the anterior portion of the intestine has many slender, blind tubes, the **pyloric caeca,** which secrete digestive enzymes. Other digestive enzymes are secreted by the inner walls of the intestine and the **pancreas.** Another organ important in digestion is the **liver,** which secretes **bile** needed for the breakdown of fats. The liver is particularly large and oil-rich in sharks, sometimes making up as much as 20% of their body weight.

A few fishes lack a stomach and tend to have a portion of the intestine expanded for the digestion of food. Carnivorous fishes have short, straight intestines. Fishes that eat seaweeds, which are more difficult to digest, have coiled intestines, which may be much longer than the fish itself. The intestines of



(a) **Cartilaginous fishes**



(b) **Bony fishes**

FIGURE 8.14 The digestive systems of (*a*) cartilaginous and (*b*) bony fishes display many of the basic features found in all vertebrates.

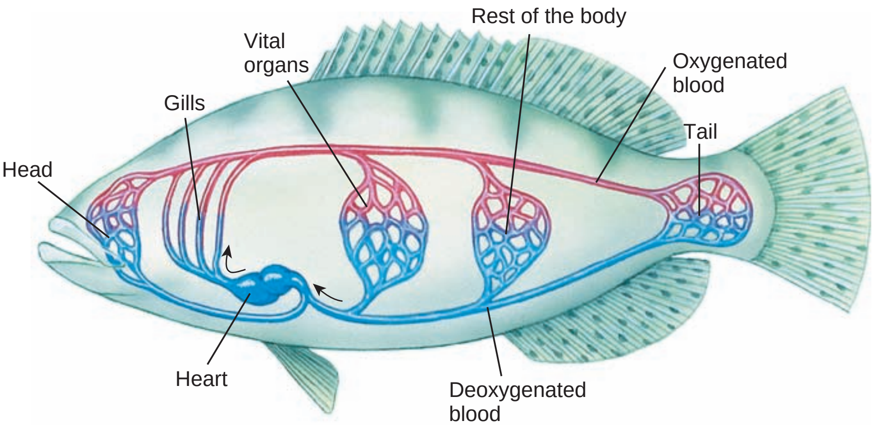


FIGURE 8.15 The circulatory system of fishes consists of veins that carry deoxygenated blood (in blue) from the body, a two-chambered heart that pumps blood to the gills for oxygenation, and arteries that carry oxygenated blood (in red) to the rest of the body.

cartilaginous fishes and a few primitive bony fishes contain a spiraling portion called the **spiral valve,** which increases the internal surface area of the intestine (Fig. 8.14*a*). The intestine is responsible for absorbing the nutrients resulting from digestion. These nutrients pass into the blood to be distributed through the body. Undigested material exits through the anus, or the **cloaca,** the common passage for the digestive, excretory, and reproductive systems in cartilaginous fishes (Fig. 8.14*a*).

Circulatory System

All fishes have a two-chambered **heart** located below the gills (Fig. 8.15). Deoxygenated blood enters the first chamber of the heart from the body. The blood is then pumped to the second chamber, which then pumps it to the gills, where **gas exchange** takes place. The oxygenated blood is then carried back to the body by blood vessels called **arteries.** The arteries branch out into thin-walled **capillaries,** which allow oxygen and nutrients to reach every cell. Other capillaries then collect into larger blood vessels, **veins,** which carry deoxygenated blood, along with dissolved carbon dioxide, back to the heart to complete the cycle.

Respiratory System

Fishes obtain oxygen dissolved in water and release carbon dioxide from their blood through paired gills. The gills lie in the pharynx, a chamber just behind the mouth that represents the front part of the gut.

Irrigation of the Gills Fishes get the oxygen they need by extracting it from the water. To do this, they must make sure that water flows over the gills—that is, they must irrigate, or ventilate, the gills.

Most sharks swim continuously. Swimming, plus the opening and closing of the mouth, forces water through the mouth, over the gills, and out through the gill slits (Fig. 8.16*a*). When caught in fishing nets, sharks cannot swim to force the water in and therefore "drown." Not all sharks need to swim, however. Nurse sharks (*Ginglymostoma*) and several other sharks rest on the bottom during the day (see Fig. 8.4*c*). They force water over the gills by opening and closing the mouth.

Expansion and contraction of the walls of the pharynx and the gill slits assist in the irrigation of gills in sharks. Every gill lies in its own chamber, and each gill chamber opens to the outside by a separate gill slit. The first pair of gill slits of cartilaginous fishes is modified into **spiracles,** a pair of round openings just behind each eye. The spiracles are located on the dorsal surface of rays and skates (see Fig. 8.6*b*). They allow these fishes, many of which live on the bottom, to take in water even when the ventral mouth is buried in the sediment. When lampreys and

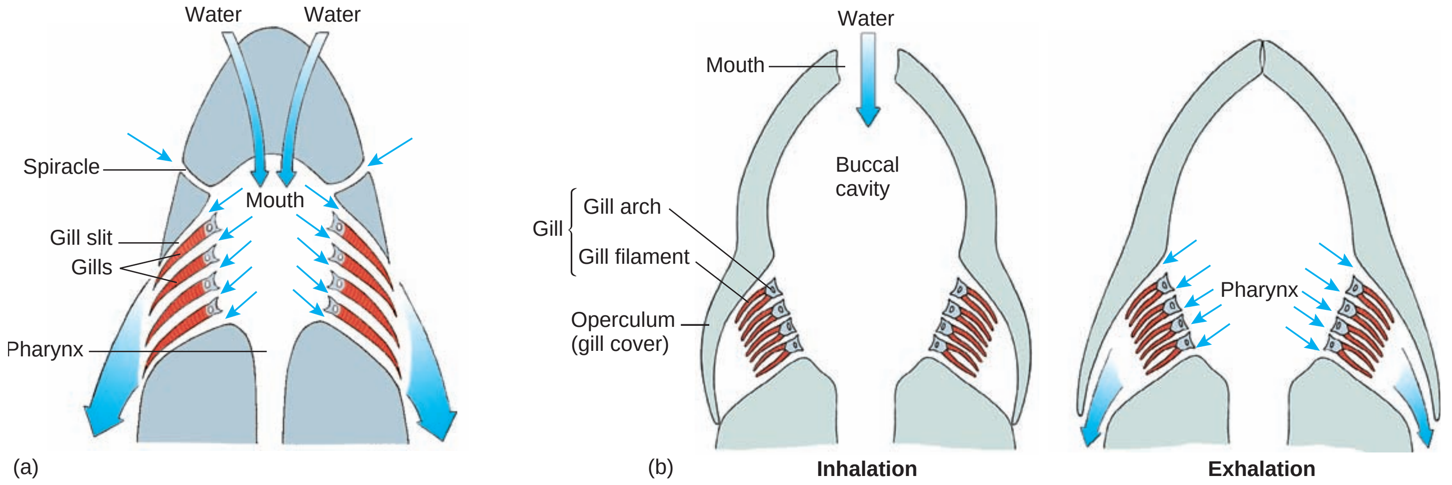


FIGURE 8.16 The mechanism behind the irrigation of the gills. (*a*) Cartilaginous fishes like sharks allow water in (path of water indicated by arrows) by opening the mouth, which is then closed. The rising of the floor of the mouth causes water to be pumped through the gills and out by way of the separate gill slits. The spiracles also allow water to move in; in rays and skates these play a crucial role. (*b*) Bony fishes are more efficient because of the presence of opercula, which close as the pharynx expands, sucking the water in. The closing of the mouth and the opening of the opercula force water through the gills and out.

other jawless fishes feed by sucking on other fishes, the passage of water through their mouth is blocked and they pump water in as well as out through the gill slits.

Most bony fishes have a more efficient mechanism to bring in water to the gills. The gills on each side share a gill chamber, which opens to the outside through an opening on each side of the head. Each opening is covered by an operculum (Fig. 8.16*b*). When the mouth opens, the opercula close and the pharynx expands, sucking water in. The fish does the reverse to pump water out: the mouth closes, the pharynx contracts, and the opercula open. Some fast swimmers simplify things by just opening their mouths to force water into the gills.

Structure of the Gills Fish gills are supported by cartilaginous or bony structures, the gill arches (Fig. 8.17*b*). Each gill arch bears two rows of slender, fleshy projections called **gill filaments.** Gill rakers project along the inner surface of the gill arch. They prevent food particles from entering and injuring the gill filaments or may be specialized for filtering the water in filter-feeding fishes.

The gill filaments have a rich supply of capillaries (Fig. 8.17*c*), the oxygenated blood of which gives them a bright red color. Each gill filament contains many rows of thin plates or disks called **lamellae,** which contain capillaries. The lamellae greatly increase the surface area through which gas exchange can take place. The number of lamellae is greater in active swimmers, which need large supplies of oxygen.

Gas Exchange Oxygen dissolved in the water diffuses into the capillaries of the gill filaments to oxygenate the blood. **Diffusion** will take place only if oxygen is more concentrated in the water than in the blood. This is usually true because the blood coming to the gills has already traveled through the rest of the body and is depleted of oxygen (Fig. 8.15). As oxygen diffuses from the water to blood in the capillaries, the amount of oxygen in the water decreases and that in the blood increases. This can reduce the efficiency of gas exchange, which depends on the water having more oxygen than the blood. Fishes, however, have evolved a clever adaptation called a **countercurrent system of flow** to increase efficiency. The blood in the gills flows in the *opposite* direction to the water passing over them (Fig. 8.17*d*). When the water has passed over the gill and given up much of its oxygen, it meets blood that has just come from the body and is "hungry" for what oxygen remains in the water (Fig. 8.17*e*). By the time the blood has flowed most of the way through the gill, picking up oxygen, it encounters water that is just entering the gill chamber and is rich in oxygen. Thus, the oxygen content of the water is always higher than that of the blood. This system makes the gills very efficient at extracting oxygen. Without this countercurrent system, blood returning to the body would have less oxygen.

The blood disposes of its carbon dioxide using the same mechanism. Blood flowing into the gills from the body has a high concentration of carbon dioxide, a product of respiration. It easily diffuses out into the water.

Gas exchange in the gills of fishes is highly efficient. The surface area of gills is greatly increased by lamellae, and the flow of water through them is in a direction opposite to that of blood.

Gas Exchange The absorption of oxygen to be used in respiration (the breakdown of glucose to release energy) and the elimination of carbon dioxide that results from the same process.
- Chapter 7, p. 126

Diffusion The movement of molecules from areas of high concentration to areas of low concentration.
- Chapter 4, p. 72

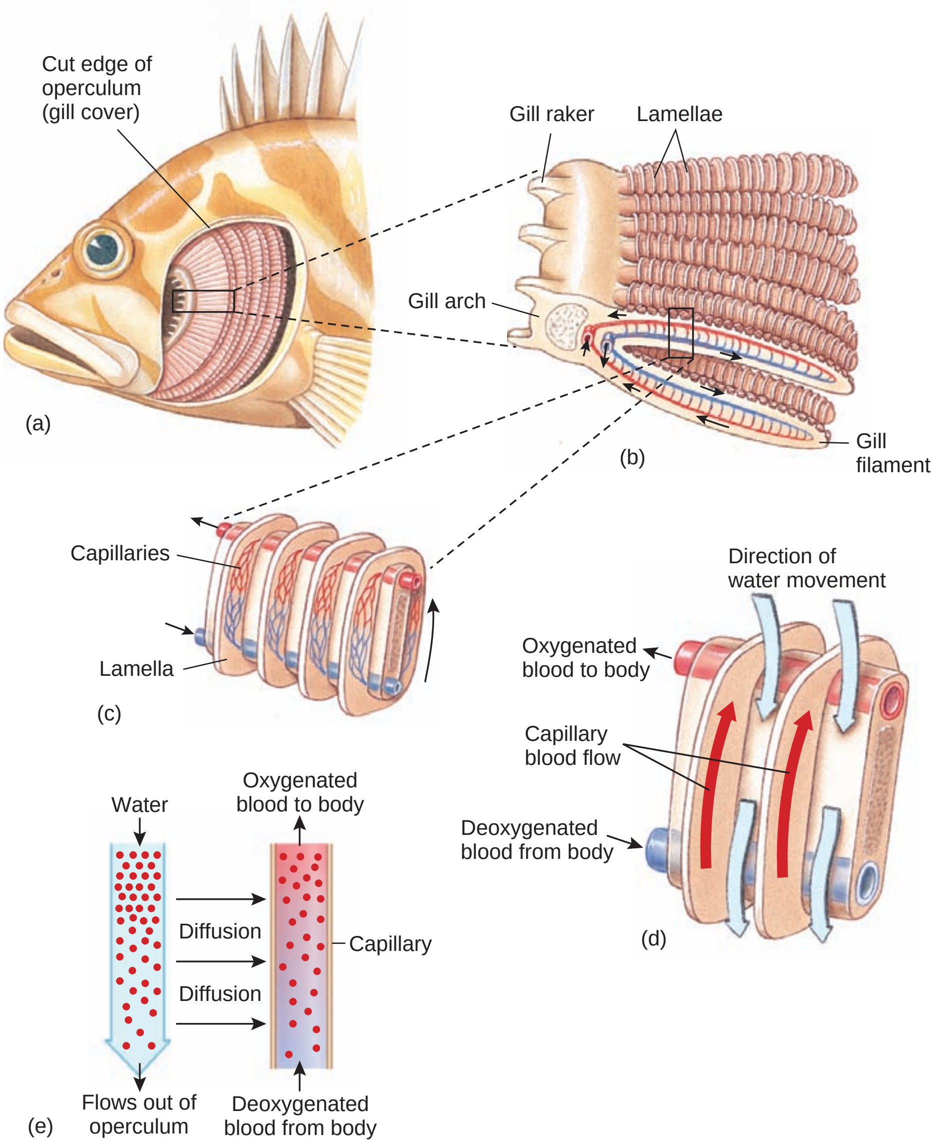


FIGURE 8.17 The gills of fishes are very efficient structures for gas exchange. Bony fishes have four pairs of gills (*a*), each containing two rows of numerous gill filaments (*b*). Lamellae in the gill filaments (*c*) increase the surface area of the gill filaments. (*d*) Diffusion of oxygen from seawater into the blood gets a boost because the water flows across the lamellae in the opposite direction to that of the blood. (*e*) The concentration of oxygen (indicated by dots) is always higher in the water than in the blood. If circulation were not reversed, blood to the body would have less oxygen.

Once oxygen enters the blood it is carried through the body by **hemoglobin,** a red protein that gives blood its characteristic color. Hemoglobin is contained in specialized cells called **erythrocytes,** or **red blood cells.** The hemoglobin releases oxygen to the tissues as it is needed. After it gives off its oxygen, the hemoglobin picks up carbon dioxide from the body and carries it to the gills, where it diffuses into the water.

Muscles use a lot of oxygen during exertion. They have a protein, called **myoglobin,** similar to hemoglobin, that can store oxygen. Hard-working muscles tend to have a lot of myoglobin, which makes them dark red. Strong swimmers, such as open-water sharks and tunas, have a high proportion of red muscle, as opposed to white muscle (see "Swimming: The Need for Speed," p. 341). Many other fishes have concentrations of red muscles at the base of heavily used fins.

Regulation of the Internal Environment

In contrast to most marine organisms, the blood of marine bony fishes is less salty than seawater (see Fig. 4.14). As a result, they lose water by **osmosis.** Marine bony fishes therefore need to **osmoregulate** to prevent dehydration. To replace lost water, they swallow seawater (Fig. 8.18*b*). Seawater contains excess salts, some of which pass straight through the gut without being absorbed. Salts that are absorbed are excreted by the **kidneys,** the most important excretory organs of vertebrates, and specialized **chloride cells** in the gills. The kidneys conserve water by producing only small amounts of urine.

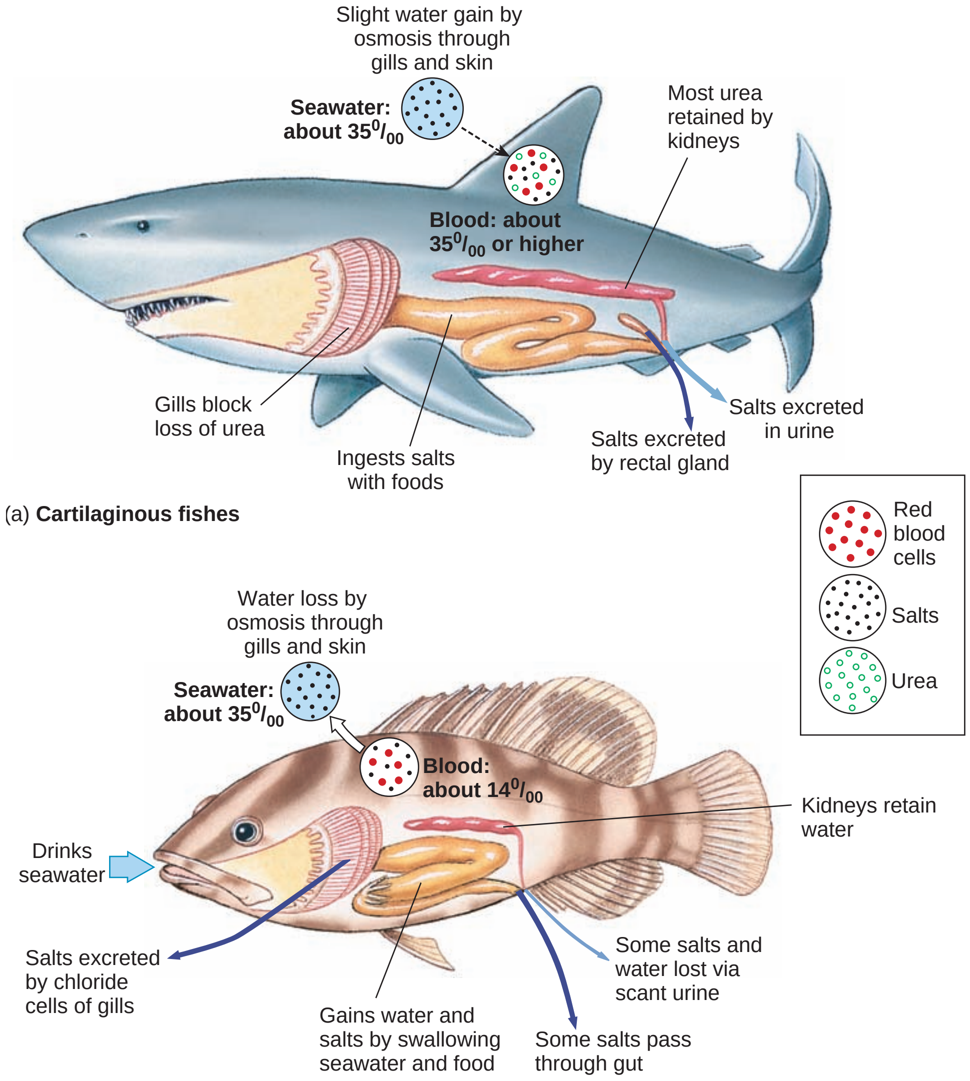
Cartilaginous fishes use a different approach to salt balance (Fig. 8.18*a*). They reduce osmosis by increasing the amount of dissolved molecules, or **solutes,** in their blood, making the blood concentration closer to that of seawater. They do this by retaining a chemical called **urea,** a waste product that results from the breakdown of proteins. The amount of urea in the blood is controlled by the kidneys. In most animals urea is toxic and is excreted, but sharks and other cartilaginous fishes excrete only small amounts. Urea and related compounds are less toxic to cartilaginous fishes. They retain most of the urea in their blood; their gills help in this process by blocking the loss of urea.

Cartilaginous fishes also absorb water to prevent dehydration, mostly through the gills and from food. Excess salts are excreted by the kidneys, intestine, and a special gland near the anus called the **rectal gland** (Fig. 8.18*a*).

Marine fishes keep a constant internal environment and check water loss through the osmoregulatory activities of the kidneys, gills, and other mechanisms.

Nervous System and Sensory Organs

Vertebrates have the most complex and advanced nervous systems of any animal group. At the heart of the system is the **central nervous system,** consisting of the brain and spinal cord. The central nervous system coordinates and integrates all body activities and stores information. The brain is divided into several regions known to serve as centers for particular functions such as


Slight water gain by osmosis through gills and skin
Seawater: about 35‰
Most urea retained by kidneys
Blood: about 35‰ or higher
Gills block loss of urea
Ingests salts with foods
Salts excreted by rectal gland
Salts excreted in urine
Red blood cells
Salts
Urea
Water loss by osmosis through gills and skin
Seawater: about 35‰
Blood: about 14‰
Kidneys retain water
Drinks seawater
Salts excreted by chloride cells of gills
Gains water and salts by swallowing seawater and food
Some salts pass through gut
Some salts and water lost via scant urine

(a) **Cartilaginous fishes**

(b) **Bony fishes**

FIGURE 8.18 Marine fishes live in water that is saltier than their body fluids. For this reason, water tends to diffuse out of the body. (*a*) To prevent dehydration, sharks and other cartilaginous fishes concentrate urea, absorb seawater through their gills and skin, and excrete excess salts by way of the urine and feces. A special gland, the rectal gland, also excretes excess salts. Their blood ends up with a solute concentration almost equal to or even higher than that of seawater. (*b*) Marine bony fishes do not concentrate urea, which is toxic to them. Instead, their kidneys conserve water, and they drink seawater, excreting excess salts, as do cartilaginous fishes, but using different organs. Compare with Figure 4.14.

olfaction and vision. It is protected by a cartilaginous or bony skull. Nerves connect the central nervous system with various organs of the body and with sense organs that receive information from the surroundings. This information is sent to the brain in the form of nerve impulses.

Most fishes have a highly developed sense of smell, which they use to detect food, mates, and predators, and sometimes to find their way home. Fishes do this with special sensory cells located in **olfactory sacs** on both sides of the head. Each sac opens to the outside through one or two openings, the nostrils, or **nares.**

The sense of smell is particularly well developed in sharks. They can detect blood and other substances in concentrations as low as fractions of one part per million. Salmon (*Oncorhynchus*), which live as adults at sea but reproduce in fresh water, use olfaction to find the stream where they were born years earlier (see "Migrations," p. 168). They accomplish part of this remarkable feat by memorizing the sequence of smells on their way out to sea.

Fishes detect other chemical stimuli with **taste buds** located in the mouth and on the lips, fins, and skin. Taste buds also are found on **barbels,** whisker-like organs near the mouth of many bottom feeders such as marine catfishes (*Arius*). Fishes that have barbels use them to detect food on the bottom.

Fish eyes are not very different from those of vertebrates that live on land. One important difference, though, is the way they focus. Whereas the eyes of most land vertebrates focus by changing the shape of the lens, the round lens of the fish eye focuses by moving closer to or farther away from the subject. This is partially why fish eyes tend to bulge. Bony fishes appear to rely on vision more than most cartilaginous fishes. Many bony fishes—particularly shallow-water species—have color vision, but most cartilaginous fishes have little or none. Some sharks have a distinct **nictitating membrane** that can be drawn across the eye to reduce brightness and to protect the eye during feeding.

Fishes have a unique sense organ called the **lateral line** that enables them to detect vibrations in the water. The lateral line consists of a system of small canals that run along the head and body (Fig. 8.19). The canals lie in the skin and in the bone or cartilage of the head. They are lined with clusters of sensory cells, or **neuromasts,** that are sensitive to vibration. The canals usually open to the surface through pores that are quite visible.

The lateral line system picks up vibrations resulting from the swimming of other animals as well as water displacements caused by sound waves. It allows fishes to avoid obstacles and predators, detect prey, orient to currents, and keep their position in a school.

Osmosis The diffusion of water across a selectively permeable membrane, such as a cell membrane.

- Chapter 4, p. 72

Osmoregulation The active control by an organism of its internal *solute* concentration to avoid osmotic problems.

- Chapter 4, p. 74

EYE ON SCIENCE

Vision in Billfishes

Marlins (*Makaira*), sailfishes (*Istiophorus*), and the swordfish (*Xiphias gladius*), collectively known as billfishes, are large, fast-swimming predators in open water. Among adaptations for high speed are their streamlined shapes and the high efficiency of their muscles (see "Swimming Machines," p. 345). Billfishes rely on their vision for hunting. They must locate and track their fast-swimming prey—squids and fishes—in the open ocean, at times in deep, dark, and cold water. Their large eyes, among the largest of all vertebrates, are an indication of the importance of vision in billfishes. Surprisingly, not much is known on how vision actually works among billfishes and other open-water predators such as tunas, but current research is revealing some fascinating details.

Almost a third of the brain of marlins is devoted to the analysis of information received from the eyes. The large size of their eyes is not an adaptation to see more detail, as one may expect, but to increase sensitivity to light to allow billfishes to distinguish prey in the faint light of the deep. Visual acuity in marlins is as high as that of many other fishes. The build of their eyes suggests that they can, for instance, resolve a 10 cm (4 in) object from a distance of 50 m (165 ft), which is comparable to that of many other fishes. The marlin eye, however, is particularly sensitive to light. The retina that lines the back of the eye contains many ganglion cells, which are in charge of sending messages to the brain. Two regions in the retina have a high concentration of ganglion cells: one region receives information about the area in front of the fish, and a second helps the marlin see particularly well what is behind without having to turn its eyes or body. The key to the high light sensitivity of the marlin's eye is that each of the many ganglion cells receives information not from one but from many of the light-sensitive cells also found in the retina.

Swordfish heat up their eyes to between 19° and 28°C (66° and 82°F), up to 15°C warmer than the temperature of the water surrounding them. They do this to further increase their ability to track prey in cold water. Part of one of the muscles that move each eye generates heat, warming up the blood in the eye as well as in the brain. Working on research vessels, Dr. Kerstin Fritsches from the University of Queensland in Australia removed retinas from freshly caught swordfish to investigate how the warming of the eyes improves the fish's vision. The retinas were kept at different temperatures and exposed to different frequencies of light flashes. Nerve impulses from retinas that were triggered by the light flashes were then measured and analyzed. The results showed that retinas were faster in transmitting impulses at the higher temperatures, like those actually found in the eyes, than at the lower temperatures found in deep water. Higher eye temperatures may prevent a slowdown in the retinal efficiency as temperatures decrease with depth. In a swordfish searching for food at 300 m (990 ft) at a water temperature of 3°C (37°F) but with a retinal temperature of 20°C (68°F), retinas are seven times more efficient in tracking fast-moving prey than are normal fish retinas with lower temperatures similar to those of the surrounding water.

Future research seeks to find out if some of the deep-water squids and fishes that billfishes prey upon have evolved adaptations that allow them to see an approaching billfish. Research on vision in billfishes may have significant applications. If other open-water fishes and sea turtles can detect certain colors of light different to those seen by the target fish, such colors might be used to deter these species from being caught and killed in longlines, a major source of wasteful by-catch (see p. 388).

How can it be shown experimentally if a marine animal can see certain colors of light? What kind of adaptations you think may have evolved in a deep-sea squid to evade predation by billfishes?

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

A swordfish (*Xiphias gladius*) eye.

Cartilaginous fishes also have sense organs in the head called the **ampullae of Lorenzini** (see Fig. 8.3) that can detect weak electrical fields. This system helps them locate prey. It may also help in navigation as a sort of electromagnetic compass or perhaps a detector of currents.

Fishes can also perceive sound waves with their **inner ears,** paired hearing organs located to the sides of the brain just behind the eyes. The inner ears are a set of fluid-filled canals that contain sensory cells similar to those in the lateral line canals. In some fishes the swim bladder amplifies sound by vibrating and

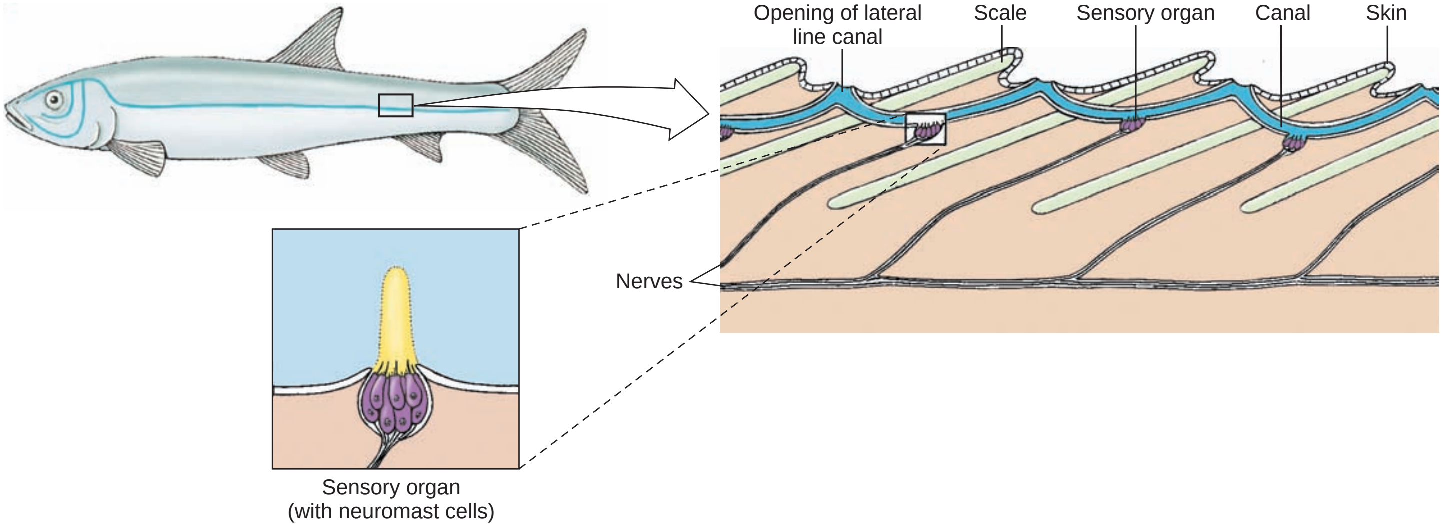

Opening of lateral line canal
Scale
Sensory organ
Canal
Skin
Nerves
Sensory organ (with neuromast cells)

FIGURE 8.19 Cross section through the skin of a fish, showing the lateral line sensory system. Notice the sensory organs opening into the canals. The nerve collects nerve impulses from the sensory organs and transmits the information to the brain.

transmitting sound waves to the inner ear. The inner ear is also involved in equilibrium and balance. Many fishes detect changes in body position from the movement of calcareous **ear stones,** or **otoliths,** that rest on sensory hairs, a mechanism similar to the **statocysts** of invertebrates.

The sense organs of fishes include eyes, olfactory sacs, taste buds, and inner ears, as well as a lateral line and other specialized organs that pick up vibrations or electrical stimuli from the water.

Behavior

Nearly all aspects of the lives of fishes involve complex behavior to adapt to light and currents, to find food and shelter, and to avoid predators. Behavior is also an important part of fish courtship and reproduction, which are described in the next section. This section provides only a glimpse of some aspects of fish behavior; some other highlights are discussed in other chapters.

Territoriality Many marine fishes, particularly open-water species, do not reside in any particular area. Others, however, are known to establish **territories,** home areas that they defend against intruders. Some fishes defend territories only during reproduction. Many others have more or less permanent territories that they use for feeding and resting or as shelter. It is thought that fishes often guard territories to ensure that they have enough food and other resources. Thus, territoriality is most common in crowded environments like kelp beds and coral reefs, where resources are most likely to be in short supply. Coral reef damselfishes are famous for fiercely defending their territories, often attacking fishes many times their size or even divers.

Fishes use a variety of **aggressive behaviors** to defend their territories. Actual fights are surprisingly rare. Instead, fishes usually prefer to avoid risking injury by bluffing. Raised fins, an open mouth, and rapid darting about are examples of such threatening postures. Territorial defense may also involve sound production. Marine bony fishes may make sound by grinding their teeth or rubbing bones or fin spines on another bone. Some fishes "drum" by pulling muscles on the swim bladder, and this sound is amplified by the air-filled bladder.

Sometimes a solitary individual defends a territory. In other species, like some butterflyfishes, territories are established by a male-female pair. Territories may also be inhabited by groups that belong to the same species. This is the case in many damselfishes, which inhabit spaces between the branches of corals (Fig. 8.20), and anemonefishes, or clownfishes (*Amphiprion;* see Fig. 14.35). Members of such groups often divide the territory into subterritories.

Schooling Many fishes form well-defined groups, or **schools.** Some, including herrings, sardines, mullets (*Mugil*), and some mackerels, school throughout their lives. Others are part-time schoolers, especially as juveniles or during feeding. Most cartilaginous fishes are solitary, but a few, such as hammerhead sharks, mantas, and other rays, sometimes travel in schools. It has been estimated that around 4,000 species, including both marine and freshwater species, school as adults. Schools can be huge, as large as 4,580 million m^3 (161,720 ft^3) in the Atlantic herring (*Clupea harengus*). The members of a school are typically all about the same size. The stationary schools that are common around coral reefs, kelp beds, rocks, and shipwrecks, however, may include members of different sizes or even different species.

Schools function as well-coordinated units, though they appear to have no leaders (Fig. 8.21). The individual fishes tend to keep a constant distance between themselves, turning, stopping,

Statocysts Sense organs of many invertebrates consisting of one or more grains or hard bodies surrounded by sensitive hairs and used to orient the animal with gravity.
- Chapter 7, p. 122

FIGURE 8.20 Some damselfishes, such as species of *Anthias* and *Chromis,* live among corals. They dash into the spaces between the coral branches whenever danger approaches.

and starting in near perfect unison. Vision plays an important role in the orientation of individuals within a school. In some species, though, blinded fish can school in a coordinated way. These fish probably use the lateral line, olfaction, and sound they emit to keep track of each other. The tight coordination of schooling fishes may break down when they are feeding or attacked by a predator.

Why do fishes school? One explanation is that schooling offers protection against predation. Predators may be confused if, for instance, the school circles a predator (Fig. 8.21*c*) or splits into several groups. It is also difficult for a predator to aim for just one fish in a cloud of shifting, darting individuals (Fig. 8.21*d*). On the other hand, some predators, such as jacks (*Caranx*), are more efficient when they attack schools of prey rather than individuals. It also has been suggested that schooling increases swimming efficiency because the fish in front form an eddy that reduces water resistance for those behind. There is experimental evidence, however, that this is not always the case and that fish do not always align in a hydrodynamically efficient way. In at least some fishes, schooling is advantageous in feeding or mating. There is probably no single reason that fishes school, and the reasons probably vary from species to species.

Migrations Another fascinating aspect of the behavior of marine fishes is **migration,** regular mass movements from one place to another once a day, once a year, or once in a lifetime. Schools of parrotfishes and other fishes migrate onshore and offshore to feed. Many open-water fishes migrate several hundred meters up and down the water column every day (see "Vertical Migration," p. 342). The most spectacular migrations, however, are the transoceanic journeys made by tunas, salmon, and other fishes. We still know little about why fishes migrate, but most migrations to be related to feeding or reproduction.

There is little doubt that feeding is the main reason behind the migration of open-water species like tunas. Recaptures of tagged fish have provided much information on how far, how fast, and when tunas migrate (see "Swimming: The Need for Speed," p. 341). Though essentially tropical, some species migrate long distances to feed in temperate waters. Such is the case in the skipjack tuna (*Katsuwonus pelamis;* Fig. 8.22) and other tunas.

Also amazing are the migrations between the sea and fresh water undertaken by some fishes that are dependent on fresh water for reproduction. **Anadromous** fishes spend most of their lives at sea but migrate to fresh water to breed. Sturgeons (*Acipenser*), whose eggs are eaten as caviar, some lampreys, and smelts (*Osmerus*) are examples. By far the best known anadromous fish, however, is the salmon.

There are seven species of salmon in the Pacific, each known by several common names. They spend their adult lives in the North Pacific, traveling thousands of miles in vast sweeps along the coast, the Aleutian Islands, and the open sea (Fig. 8.22). Some even venture into the Bering Sea and the Arctic Ocean.

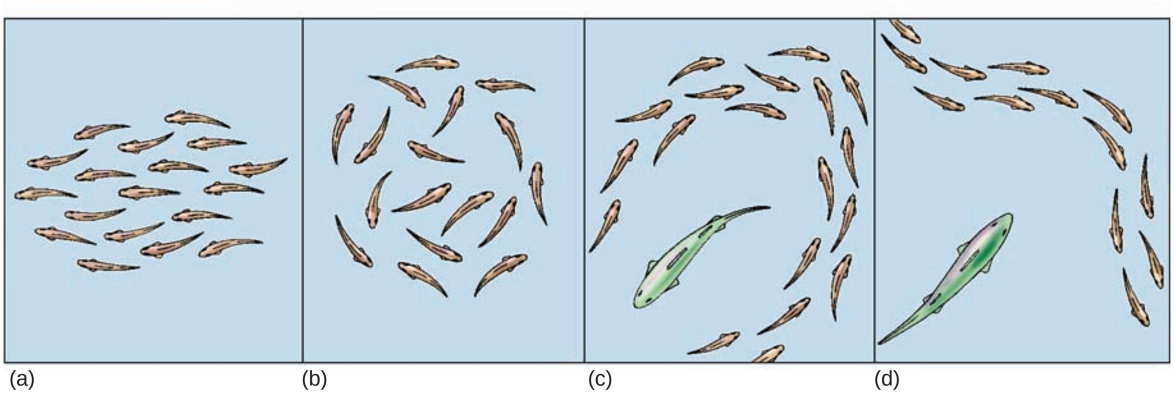


FIGURE 8.21 Fishes follow different recognizable patterns when schooling. Some common patterns include (*a*) traveling, (*b*) feeding on plankton, (*c*) encirclement of a predator, and (*d*) streaming to avoid a predator.

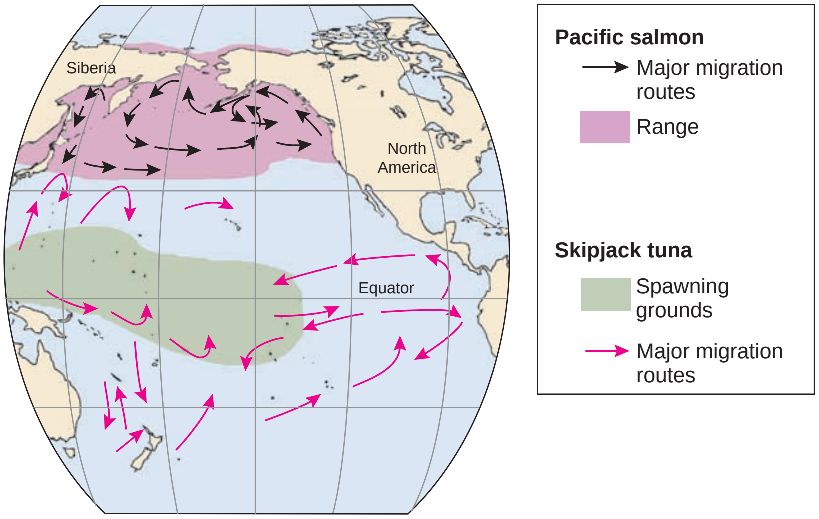


FIGURE 8.22 The skipjack tuna (*Katsuwonus pelamis*), the leading commercial catch among tunas, undertakes extensive migrations that every year take it almost halfway across the globe. The Pacific salmon (*Oncorhynchus*) migrates to spawn only once in a lifetime. Approximate limits of distribution and migration routes indicated are for all seven species of salmon.

How they navigate at sea is not known. It has been hypothesized that they use land features at least part of the way. Currents, salinity, temperature, and other water characteristics might provide clues. Other possibilities include orientation to polarized light, the sun, or the earth's magnetic field.

After several years at sea, a period characteristic of each species, salmon mature sexually and start migrating into rivers. They are probably guided at first by the earth's magnetic field. They do not feed once they enter fresh water, living instead on stored fat. Their kidneys must adjust to the change from salt to fresh water. Eventually, they reach the exact stream of their birth, sometimes far upstream (Fig. 8.23). The king, or chinook, salmon (*Oncorhynchus tschawytscha*) and chum, or dog, salmon (*O. keta*) reach as far inland as Idaho and the headwaters of the Yukon River.

Salmon find their home streams with remarkable accuracy, using a type of chemical memory. They recognize not only the "smell" of their own stream but also those of other streams they pass along the way. There also is evidence that they respond to chemicals released by other members of their own species. The ability of an animal to find its way back to a home area is known as **homing behavior.**

Salmon spawn on beds of clean gravel in the shallows. The female digs out a shallow nest, or "redd," into which she deposits her eggs. The eggs are fertilized by the male and covered with gravel. After defending the nest for a while, the salmon die.

After hatching, the young salmon may return to sea immediately, as in the pink, or humpback, salmon (*O. gorbuscha*). The young of other species remain in fresh water for a time, as long as five years for the sockeye, or red, salmon (*O. nerka*). The kokanee salmon, a race of this last species, is landlocked and does not migrate to sea at all.

One of the biggest hazards Pacific salmon endure is the destruction of their natural environment by humans. Migration routes have been blocked by dams, spawning grounds filled with silt as a result of logging and cattle grazing, and rivers polluted by pesticides (which, among other toxic effects, are suspected of disrupting salmon's sense of smell), fertilizers, and animal waste. So serious is the problem that sharp restrictions have been imposed on the harvest of salmon along the Pacific coast of the United States. Some species, like the sockeye, king, and chum salmon, have been declared endangered in some rivers. Around 11 to 15 million salmon once spawned in the Columbia River system in the northwestern United States. The number has now decreased by 90%, and most of the returning adults were born in hatcheries.

The Atlantic salmon (*Salmo salar*) breeds on both sides of the North Atlantic. It migrates across the ocean, mostly off Greenland, before returning to rivers from New England to Portugal. Atlantic salmon sometimes survive after spawning and return to the ocean. Some females have made as many as four round trips. Like their Pacific cousins, populations of the Atlantic salmon in the wild are in serious decline, though they are farmed for food in some temperate regions besides the Atlantic (see Table 17.3, p. 394).

Catadromous fishes have a migratory pattern opposite that of salmon. They breed at sea and migrate into rivers to grow and

FIGURE 8.23 The journey of Pacific salmon such as these sockeye salmon (*Oncorhynchus nerka*) is an arduous one, indeed. The fish have to swim far upstream, often leaping over rapids and waterfalls. Many fall prey to hungry predators or to the nets and lines of fishers.

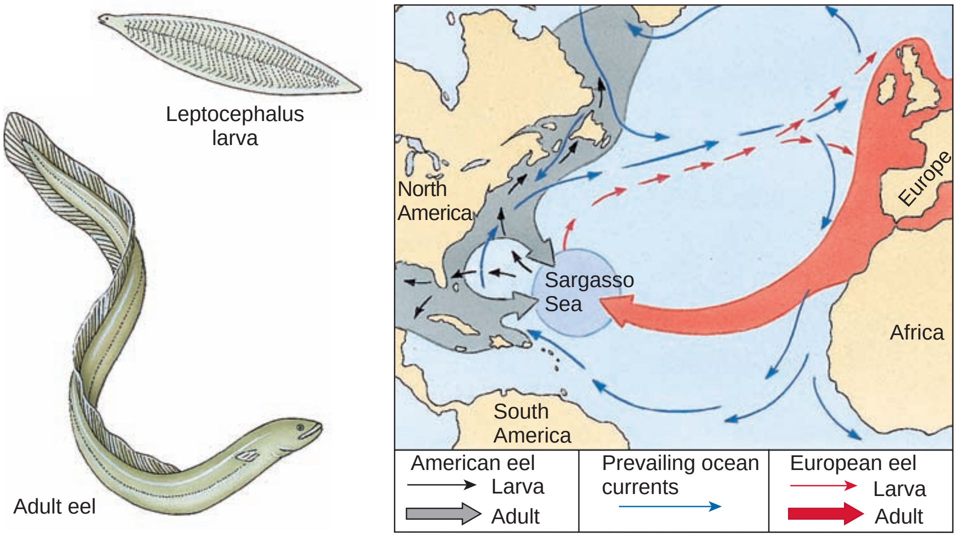


FIGURE 8.24 Two species of freshwater eels, the American (*Anguilla rostrata*) and European (*A. anguilla*) eels, breed in the Sargasso Sea and migrate to rivers in North America and Europe. The return trip of larvae is not precisely known, so the arrows indicate only the most likely routes.

mature. Several catadromous fishes are known, but the longest migration of any of them is that of freshwater eels (*Anguilla*). There are at least 16 species, including the American (*A. rostrata*) and European (*A. anguilla*) eels.

Both American and European eels spawn in the **Sargasso Sea** at depths of at least 400 to 700 m (1,300 to 2,300 ft) and then die (Fig. 8.24). They spawn at different, though overlapping, periods and locations in the sea. The eggs hatch into tiny, transparent larvae that gradually develop into elongated, leaf-shaped **leptocephalus larvae.** American eel larvae drift in the plankton for at least a year. The juveniles then move into rivers along the Atlantic coast of North America. The leptocephalus larvae of the European eel are believed to spend at least an extra two or three years drifting in the Gulf Stream to reach rivers throughout western Europe. Adults of both species eventually grow to more than 1 m (40 in) in length. Both juveniles and adults are highly valued as food, particularly in Europe. After 10 to 15 years in fresh water, adults turn silver and their eyes become larger. Soon after this, they head out to sea.

The migration of eels back to the Sargasso Sea is not completely understood. How do they navigate to reach such a distant spot? There is experimental evidence that they use the earth's magnetic field as a cue for navigation. It has been assumed that European eels follow favorable currents that take them first along the coast of northwest Africa (Fig. 8.24), much like the Portuguese navigators of old (see "Tall Ships and Surface Currents," p. 50).

Some biologists once suggested that the adults of the European eel did not return to the Sargasso Sea at all but died at sea. According to this view, American and European eels were really the same species. Larvae that remained too long at sea simply ended up drifting to Europe. We now know that this is not true and that the American and European eels are distinct species.

Reproduction and Life History

Reproduction in fishes involves a number of adaptations of the reproductive system and the behavior that brings the two sexes together and ensures successful reproduction.

Reproductive System The reproductive system of fishes is relatively simple. The sexes are usually separate. Both sexes have paired gonads located in the body cavity (see Fig. 8.14).

In cartilaginous fishes, ducts lead from the ovaries and testes into the cloaca, which opens to the outside (see Fig. 8.14*a*). Jawless and bony fishes have a separate opening for urine and gametes, the **urogenital opening,** which is located just behind the anus (see Fig. 8.14*b*).

In many marine fishes the gonads produce gametes only at certain times. The timing of gamete production is crucial. Both sexes must be ready to spawn at the same time. Spawning, as well as larval development, must take place during the period with the most favorable conditions. The exact timing of reproduction is especially critical for fishes that make long migrations to breed.

The timing of reproduction is controlled for the most part by **sex hormones.** Sex hormones are produced in the gonads and released in small amounts into the blood. They stimulate the maturation of gametes and may cause changes in color, shape, and behavior before breeding.

The release of sex hormones is triggered by environmental factors such as day length, temperature, and the availability of food. Fishes can be artificially induced to spawn when these environmental factors are controlled or when hormones are injected. This technique is used to increase reproduction in fishes grown for food (see "Mariculture," p. 392).

A few marine fishes are **hermaphrodites.** Some, like the hamlet (*Hypoplectrus*), are called **simultaneous hermaphrodites** because they can produce sperm and eggs at the same time. Though able to fertilize their own eggs, simultaneous hermaphrodites usually breed with one or more other individuals, ensuring cross-fertilization. One member of a pair of mating hamlets, for example, acts as a male and its sperm fertilizes the eggs released by the other individual. Roles are reversed after fertilization, and the "female" releases sperm to fertilize eggs released by the "male." Hermaphroditism also is found among several deep-water fishes, an adaptation to the depths of the ocean where it may be difficult to find members of the opposite sex (see "Sex in the Deep Sea," p. 369).

A variation of hermaphroditism among fishes is **sex reversal,** or **sequential hermaphroditism,** in which individuals begin life as males but change into females **(protandry)** or females change into males **(protogyny).** These changes are controlled by sex hormones but triggered by social cues such as the absence

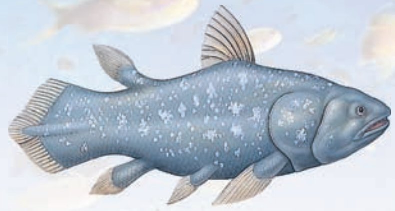
EVOLUTIONARY PERSPECTIVE

A Fish Called *Latimeria*

In December 1938 the skipper of a fishing trawler operating in deep water off the Chalumna River in South Africa found a very strange fish in his catch. He took it to Marjorie Courtnay-Latimer, a young curator at the local museum, who recognized the fish as something special. She sent a sketch of the 1.5 m (5 ft) specimen to Dr. J. L. B. Smith at nearby Rhodes University, and history was made.

The fish was a big catch, indeed. It was a **coelacanth,** a type of fish thought to have become extinct 60 million years ago. Extinction is not a rare event in evolution, and coelacanths were previously known only from fossils, some at least 400 million years old. They belong to the crossopterygian fishes, a group of fishes that might have given rise to the first land vertebrates. About 375 million years ago a crossopterygian fish with paddle-like bony fins crawled out of the water and changed life on earth forever. There is ample evidence that all present-day land vertebrates evolved from crossopterygian fishes (see "When Fishes Stepped on Land," p. 80).

Dr. Smith officially described the fish and named it *Latimeria chalumnae* in honor of its discoverer and the river near which it was caught. Unfortunately, the internal organs of the fish had been discarded by the time Dr. Smith got to it, so nothing was known of its internal structure. A reward was offered for more specimens of this incredible "living fossil," so called because it is similar to no known species other than fossils. It was not until 1952 that a second specimen was caught near the Comoro Islands, between Madagascar and mainland Africa. Ironically, the fish is well known to the natives of the islands. They eat its oily flesh after drying and salting it, and they use its rough skin for sandpaper!



The coelacanth (*Latimeria chalumnae*), a living fossil.

A live Indonesian coelacanth (*Latimeria menadoensis*).

The fish is still very rare. None of the captured specimens has survived more than 20 hours; thus, little is known about their habits. In 1987 a small submersible was used to film and observe a live *Latimeria* in its natural environment for the first time. The fish was observed only at night, at depths of 117 to 200 m (386 to 660 ft). In 2000 divers filmed several live *Latimeria* off the northeastern coast of South Africa. The fish were filmed at a depth of only 104 m (320 ft).

Latimeria is a large fish, up to 1.8 m (6 ft) in length and weighing as much as 98 kg (216 lb). The body is covered by large blue scales. It feeds on fish and squid. This living fossil is unique in many ways. It has heavy, stalked fins that have bones as land vertebrates do. The fish appears to stand on the fins, but not to crawl over the bottom with them, as once thought. The pectoral fins can rotate nearly 180 degrees, allowing the fish to swim slowly over the bottom, sometimes standing on its head or with its belly up.

Much remains to be discovered about this fascinating creature. Jelly-filled organs on the head may be used to detect electrical fields and thus help in prey location. Little is known about its reproduction. Females bear live young, and the huge eggs (about 9 cm, or 3.5 in, in diameter) develop in the reproductive tract.

Latimeria remains a priceless catch, and several aquaria around the world would like very much to capture live specimens. As their value in dollars soars, so do the concerns about the 200 individuals that may still survive in the Comoros. International trade has now been officially outlawed. More recent catches along the Indian Ocean coast of East Africa, however, indicate a wider distribution than originally thought. Specimens were caught in fishers' gill nets in Mozambique, Tanzania, and Kenya in 2003 and 2004. The South and East African specimens are genetically similar, so they are members of the same species.

In 1997 *Latimeria* surprised everybody by turning up in a fish market in Sulawesi, one of the islands of Indonesia, almost 10,000 km (6,200 mi) from the Comoros! A live specimen was taken off the same island in 1998. Though very similar in appearance to the Indian Ocean specimens, DNA evidence showed that the Indonesian coelacanth belonged to a different species than that in the Indian Ocean. The discoverer, Dr. Mark Erdmann, and the Indonesian team that had studied the specimen planned to formally describe the new species in a scientific publication. But a group headed by French scientists went ahead and, without Erdmann's knowledge, officially described the Indonesian coelacanth as a new species, *Latimeria menadoensis*. Additional Indonesian coelacanths were filmed in deep water in 2006.

Are there any new coelacanths waiting to be discovered somewhere else?

of a dominant male. Sex reversal occurs in several groups of marine fishes, but it is most prevalent among sea basses and groupers (*Serranus, Epinephelus*), parrotfishes, and wrasses. Some rather complicated reproductive strategies have been discovered among these fishes.

In at least some species of anemone-fishes (*Amphiprion*), all individuals begin as males. Each sea anemone is inhabited by a single, large female that mates only with a large, dominant male. All the other fishes that live on the anemone are small, non-breeding males. If the female disappears or is experimentally removed, her mate changes into a female and the largest of the non-breeding males becomes the new dominant male.

Sargasso Sea The area of the Atlantic Ocean north of the West Indies that is characterized by masses of drifting Sargasso weed, a brown seaweed.
- Chapter 6, p. 105

Hormones Molecules that act as chemical messengers within the body.
- Chapter 4, p. 65

The new female can start spawning as soon as 26 days after her sex change. Males of some wrasses form harems of many females. If the male disappears, the largest, dominant female immediately begins to act as a male and within a relatively short period of time changes color and transforms into one that is capable of producing sperm.

Reproductive Behavior Potential mates must get together at the right time to breed. Many species migrate and congregate in specific breeding grounds, as in the salmon and freshwater eels previously discussed. Sharks are usually loners but may come together during the breeding season. Many of them appear to stop feeding at spawning time.

Many bony fishes change color to advertise their readiness to breed. Most salmon undergo dramatic changes. Both sexes of the sockeye salmon turn from silver to bright red, giving rise to another of its common names, the red salmon. In male sockeye and pink, or humpback, salmon, the jaws grow into vicious-looking hooks. Males of the latter species also develop a large hump. Color changes also can be observed in tropical fishes. Many male wrasses, colorful all the time, appear even more spectacular before breeding.

The first step in reproduction is **courtship,** a series of behaviors that attract mates. These behaviors involve an exchange of active displays such as "dances," special postures that display colors, and upside down swimming (Fig. 8.25). Each species has a unique courtship behavior. This is thought to help keep fishes from mistakenly mating with members of the wrong species.

Reproduction in fishes involves many adaptations that help individuals get together for mating. These include migrations, the display of particular colors as sex signals, and courtship behavior.

Some fishes have **internal fertilization** of the eggs, in which the sperm is directly transferred from males to females through the act of **copulation. External fertilization,** the release of gametes into the water, or **broadcast spawning,** is more common in fishes, however.

Internal fertilization occurs mainly in cartilaginous fishes. Unfortunately, not much is known about their sex life. Male sharks, rays, and skates have a pair of copulatory organs, called **claspers,** located along the inner edge of the pelvic fins (Fig. 8.26). The typical approach of a romantic male shark consists of biting his potential mate on the back. The male copulates by inserting his claspers into the female's cloaca. He bites and hangs from her or partly coils around her middle. Some skates mate after the male bites the female's pectoral fins. He presses his ventral surface against hers and inserts the claspers.

Open-water fishes (sardines, tunas, jacks, and others) and those living around coral reefs and other inshore environments

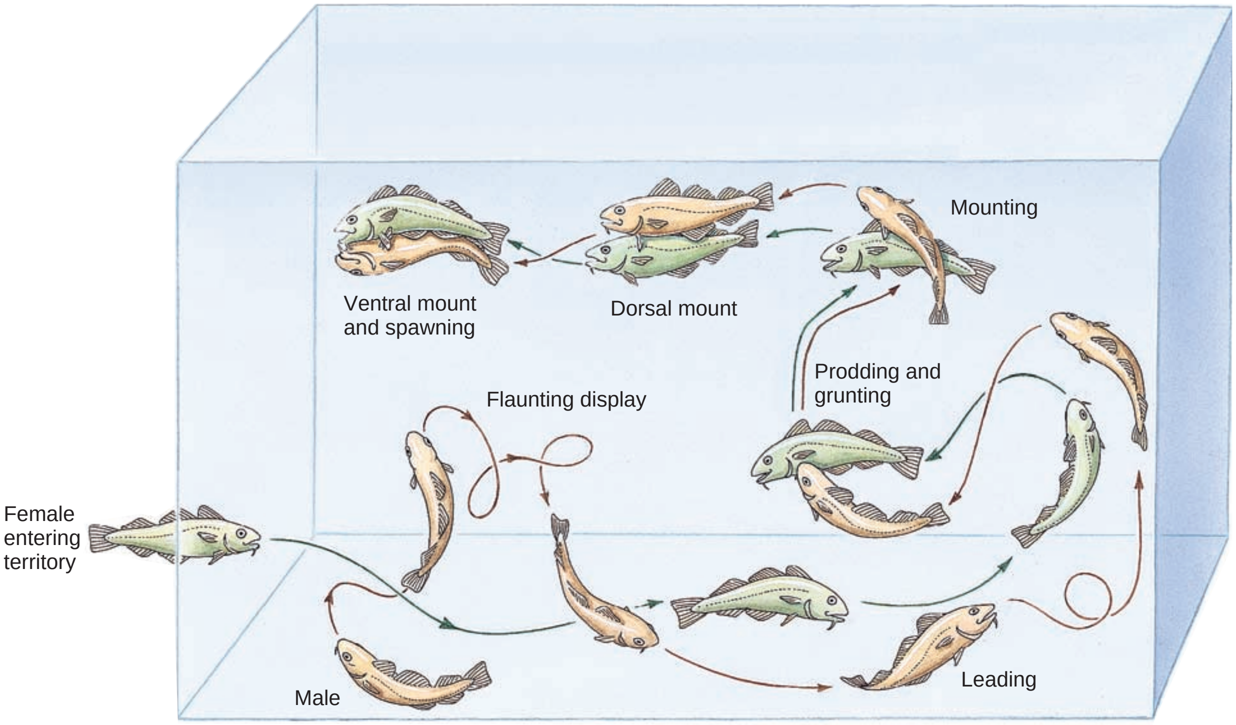


FIGURE 8.25 The Atlantic cod (*Gadus morhua*), once one of the most important food fishes in the world, spawns in large aggregations in the North Atlantic. The two sexes do not spawn indiscriminately but follow a strictly choreographed series of behaviors. The male establishes a territory, and the action starts after an interested female enters his territory. Most of the display is made by the male, which uses fully spread fins, grunting sounds, and a series of swimming behaviors. If the female does not follow the male, he has to start all over again to try to attract another female. The spawning of gametes into the water thus climaxes a series of behaviors that includes visual, sound, and tactile signals.

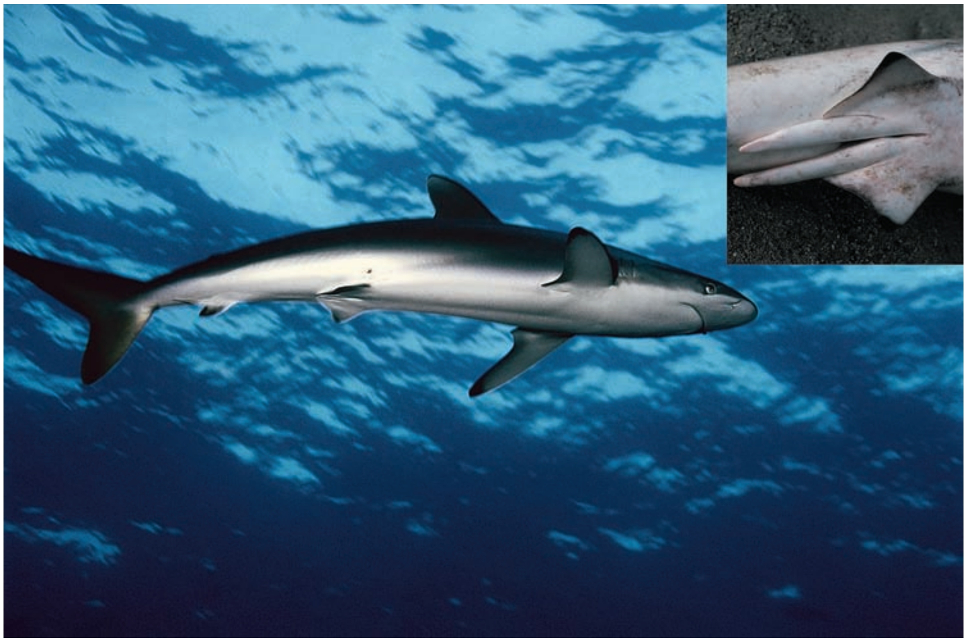


FIGURE 8.26 Fertilization in cartilaginous fishes is internal, so males must possess some type of copulatory organ. This is the function of the claspers, which are located on the inner edge of the pelvic fins. They are provided with a groove for the passage of sperm. Only one clasper is inserted into the female at a time. The photo shows a male silky shark (*Caracharhinus falciformis*); the claspers of a scalloped hammerhead shark (*Sphyrna lewini*) are shown in the inset.

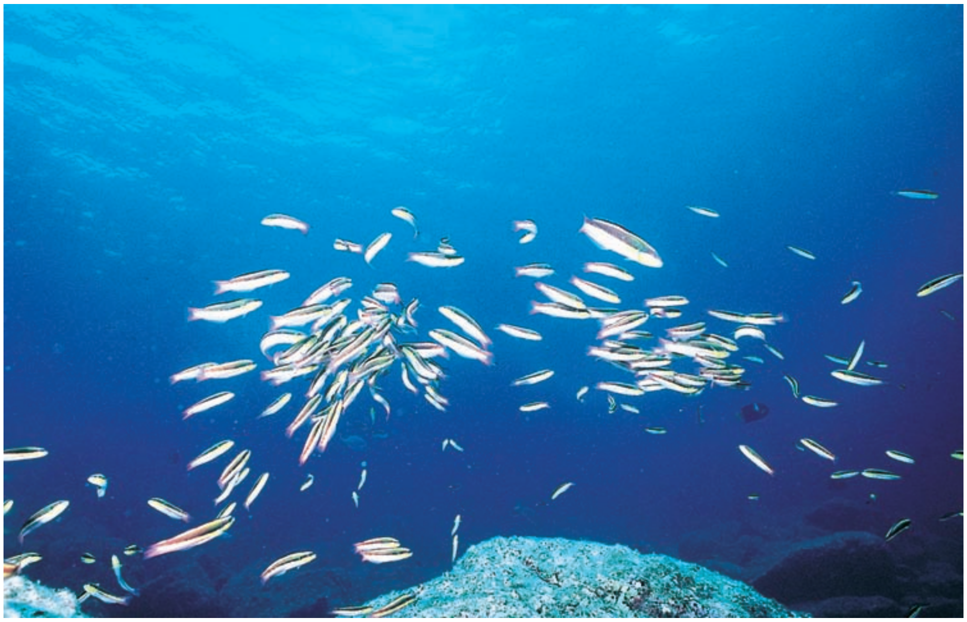


FIGURE 8.27 Males and females of the rainbow wrasse (*Thalassoma lucasanum*) from the Gulf of California swarm to release sperm and eggs.

(such as surgeonfishes, parrotfishes, and wrasses) spawn directly into the water after courtship (Fig. 8.27). Females typically release many eggs. In the Atlantic cod (*Gadus morhua*), for example, a female 1 m (40 in) long can release up to 5 million eggs. The Atlantic tarpon (*Megalops atlanticus*) releases more than 100 million eggs every time it spawns.

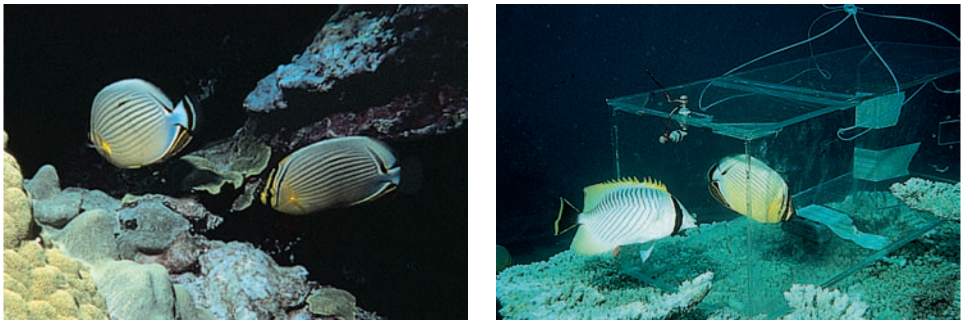
Some fishes, like butterflyfishes, spawn in pairs (Fig. 8.28), others in groups. Individual males may establish territories or aggregate into groups. Groups of males may be approached by single females or by females in groups. Usually, males seek out the females and entice them to spawn via courtship. Two individuals may pair only during spawning time, as in butterflyfishes, or may establish long-lasting bonds.

Eggs fertilized in the water column drift in currents and develop as part of the plankton. Most eggs contain oil droplets and are buoyant. Other eggs sink to the bottom. Herrings deposit their eggs on the surface of seagrasses, seaweeds, and rocks. Lampreys and salmon bury their eggs after spawning. The California grunion (*Leuresthes tenuis*) buries its eggs on sandy beaches during high tides; they don't hatch until the next high tide (see Fig. 3.30).

Most of the eggs that are released into the plankton don't survive. Fishes and other marine animals that spawn into the plankton are broadcast spawners that release as many eggs as possible to ensure that at least some hatch and make it to adulthood. Eggs require a lot of energy to produce because they must contain enough yolk to nourish the young until they hatch and can feed.

Fishes that spawn fewer and larger eggs have evolved ways to take care of them. In many damselfishes males establish and defend breeding sites or nests (Fig. 8.29) in holes among rocks or coral, empty mollusc shells, and other shelters—even discarded tires. After spawning, the eggs are retained in the nest and guarded by the males; the females leave after spawning. Males are promiscuous and will guard eggs they have fertilized from different females. Nests also are guarded by males in some gobies, blennies, and sculpins. In the Antarctic plunderfish (*Harpagifer bispinis*), the female prepares a breeding site and guards it for four to five months after spawning. If she disappears or is removed, her job is taken over by another plunderfish, usually a male.

Some fishes go even further and physically carry the eggs after they have been fertilized. Male pipefishes carry the eggs attached in neat rows to their bellies. A male seahorse literally becomes pregnant after the female deposits its eggs in a special pouch on his belly. In some cardinalfishes, marine catfishes, and other groups, males brood the fertilized eggs in their mouths (see Fig. 4.21*b*).



(a)

(b)

FIGURE 8.28 Butterflyfishes are among the most colorful of coral reef fishes. Some species use their tiny mouths (see Fig. 8.13*b*) to feed on coral. Adults of some species occur in male and female pairs. (*a*) In the oval butterflyfish (*Chaetodon trifasciatus*) pairs establish territories around coral colonies. (*b*) Experiments using transparent plastic cages provide valuable information on their behavior. Here, a caged oval butterflyfish elicits an aggressive response from an individual chevron butterflyfish (*Chaetodon trifascialis*), an indication that the caged fish has intruded in the territory of the latter. This technique can be used to map the boundaries of territories. Territorial butterflyfishes that live in pairs, like *C. trifasciatus,* fight with other pairs, but fighting occurs only between individuals of the same sex in each pair. Therefore, by using a caged fish of known sex, experimenters can determine the sex of the wild fish, which is normally impossible in the field.

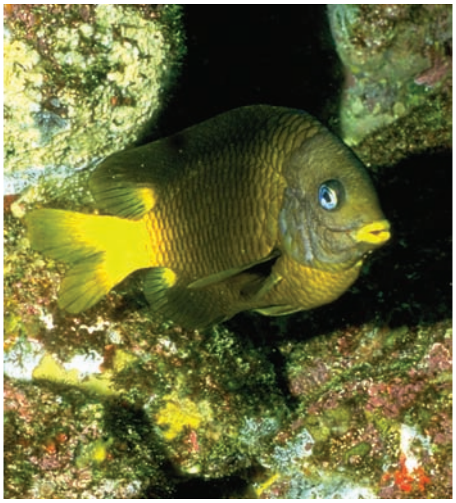
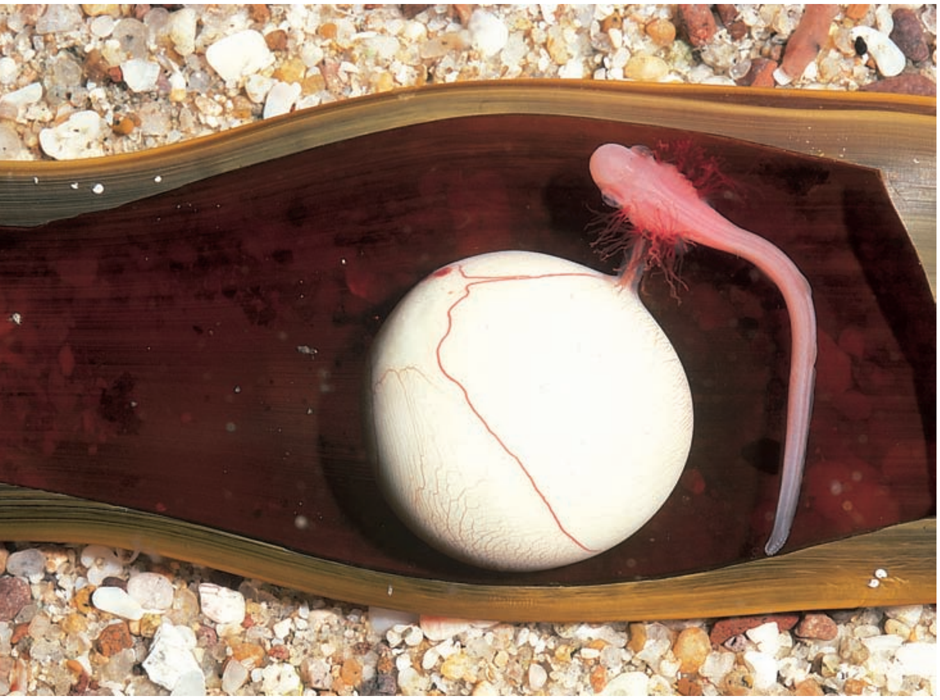


FIGURE 8.29 The yellow tail damselfish (*Stegastes arcifrons*) from the Galápagos Islands, like many other damselfishes, establishes and actively defends breeding sites where females lay their eggs.

Early Development Most fishes spawn eggs and are known as **oviparous.** In oviparous sharks, skates, and other cartilaginous fishes, the embryo is enclosed by a large, leathery egg case (the "mermaid's purse" of skates) that drops to the bottom after spawning (Fig. 8.30). About 43% of all cartilaginous fishes are oviparous. The egg cases are rather large and often have thin extensions that attach them to surfaces. Only a few are laid at a time. The eggs have a large amount of yolk in a **yolk sac** that is attached to the embryo's belly (see photo on p. 64). Yolk provides energy for several months of development, a long time by fish standards. As a result, the pup is well developed when it finally hatches.

FIGURE 8.30 An egg of the swell shark (*Cephaloscyllium ventriosum*) containing a one-month-old embryo. The large, white structure is the yolk sac. The egg case has been cut open to show the embryo.



In some cartilaginous fishes the female retains the eggs inside her reproductive tract for additional protection. The eggs develop inside the female, which gives birth to live young. Such fishes are known as **ovoviviparous.** Most ovoviviparous fishes are cartilaginous. A total of 300 embryos, still in egg cases, were found ready to emerge inside the reproductive tract of a female whale shark. Some rockfishes are among the few marine bony fishes that can be classified as ovoviviparous. Most bony fishes are oviparous and spawn their eggs for external fertilization.

In some ovoviviparous sharks, the embryos rely on other sources of nutrition once they have consumed the yolk. In the sandtiger shark (*Carcharias taurus;* see Fig. 8.3) only two pups, which are large (up to 1 m or 3.3 ft) and active, are born. Each survived in one of the two branches of its mother's reproductive tract by eating its brothers and sisters. When that source of food is gone, they consume unfertilized eggs produced by their mother's ovaries.

Some sharks and rays have embryos that actually absorb nutrients from the walls of the mother's reproductive tract. This is remarkable because it is very similar to the development of the embryo in mammals. These sharks are said to be **viviparous.** Not only are they live-bearers, but nutrition for development before birth is provided by direct contact with the reproductive tract of the female. The surfperches (*Embiotoca*), which are bony fishes, are also viviparous. Their young have large fins that absorb nutrients from the walls of the mother's uterus.

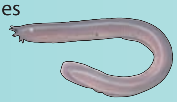
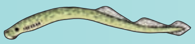
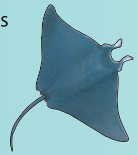
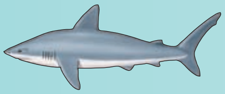
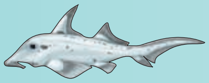
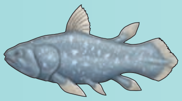
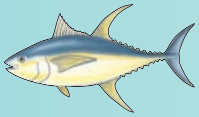
There is now evidence of yet another method of reproduction among sharks. A female bonethead shark (*Sphyrna tiburo*), a small hammerhead shark, gave birth to a pup after 3 years in an aquarium together with 2 females of the same species but no males. Though it was possible that the female had stored sperm in her body as the result of sex with a male shark prior to capture, the DNA of the pup matched the DNA of one of the 3 females with no evidence of DNA from a male. Though very rare among vertebrates, **parthenogenesis,** the development of an egg into a normal embryo without fertilization by sperm, has also been reported in a few bony fishes.

Development of the embryo proceeds rather quickly in most bony fishes. The transparent outer envelope of the eggs, the chorion, is thin, allowing oxygen to diffuse through. The eggs are usually spherical.

The embryo is supplied with nutrient-rich yolk. After one or more days of development, the eggs hatch into free-swimming larvae, or fry. When they first hatch, the larvae still carry the yolk in a yolk sac. The yolk is eventually consumed, and the larvae begin feeding. Many larvae, like the leptocephalus larvae of eels (see Fig. 8.24), do not resemble their parents at all and undergo metamorphosis to a juvenile stage that resembles the adult.

Most marine fishes are oviparous and release eggs into the water. Internal fertilization leads to ovoviviparous or viviparous conditions in some, especially cartilaginous fishes.

Table 8.1 Most Important Characteristics of Marine Fishes

Group	Distinguishing Features	Skeleton	Feeding	Reproduction	Significance in the Marine Environment
Hagfishes 	No paired fins; no scales; exposed gill slits; marine	Cartilaginous skull; no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Predators of dead or dying fishes and bottom invertebrates
Lampreys 	Two dorsal fins only; no scales; exposed gill slits; fresh-water or anadromous	Cartilaginous skull; no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Suckers of fish blood or predators of bottom invertebrates
Rays, skates 	Paired fins; placoid scales; pectoral fins greatly expanded; five ventral gill slits; mostly marine	Cartilaginous	Grinding plates to feed on bottom animals or gill rakers to filter plankton	Oviparous, viviparous	Predators of bottom animals or filter feeders
Sharks 	Paired fins; placoid scales; exposed, 5–7 lateral gill slits; mostly marine	Cartilaginous	Teeth in jaws to capture prey or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators or filter feeders
Ratfishes 	Paired fins; placoid scales; one pair of gill slits covered by flap of tissue; deep water	Cartilaginous	Grinding plates to feed on bottom invertebrates	Oviparous	Predators of bottom invertebrates
Coelocanth 	Paired fins; large scales; gills covered by operculum; deep water	Bony	Teeth in jaws to capture prey	Ovoviviparous	Predators
Bony fishes 	Paired fins; cycloid or ctenoid scales (absent in some); gills covered by operculum; marine and fresh water	Bony	Teeth in jaws to capture prey or graze or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators, grazers, and filter feeders

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge videoclips and web links to chapter-related material.

Critical Thinking

1. Hagfishes and lampreys are the only living representatives of a very ancient group. Why do you suppose there are still some of these jawless fishes around?
2. A deep-water shark, new to science, is collected for the first time. The specimen is studied in detail, but its stomach is empty. How can you get a rough idea of its feeding habits? The specimen is a female, and its reproductive tract is found to contain 20 eggs. Can you tell the type of development characteristic of this species?
3. Individuals of some species of bony fishes change sex—some to maintain more males than females, others more females than males. What are the advantages and disadvantages of each situation? Are there any advantages and disadvantages in having an equal number of males and females?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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Kemper, S., 2005. Shark. *Smithsonian,* vol. 36, no. 5, August, pp. 42–52. The survival of sharks is threatened by overfishing.

Martin, R. A. and A. Martin, 2006. Sociable killers. *Natural History,* vol. 115, no. 8, October, pp. 42–48. The social and hunting behaviors of the great white shark are far more complex than originally thought.

Shadwick, R. E., 2005. How tunas and lamnid sharks swim: An evolutionary convergence, *American Scientist,* vol. 93, no. 3, November/December, pp. 524–531. Tunas and some sharks have evolved similar adaptations to increase swimming efficiency, even if they are only distantly related.

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Summers, A., 2005. When the shark bites. *Natural History,* vol. 115, no. 2, March, pp. 30–31. Shark teeth are bioengineered to either stab or crush their prey.

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Wilson, S. G., 2006. The biggest fish. *Natural History,* vol. 115, no. 3, April, pp. 42–47. Whale sharks, the largest living fish, show signs of overfishing.

In Depth

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Lisney, T. J. and S. P. Collin, 2006. Brain morphology in large pelagic fishes: a comparison between sharks and teleosts. *Journal of Fish Biology,* vol. 68, pp. 532–554.

Montgomery, J. C., A. Jeffs, S. D. Simpson, M. Meekan, and C. Tindle, 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Advances in Marine Biology,* vol. 51, pp. 143–196.

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Male frigate bird (*Fregata magnificens*), Galápagos Islands.

9

CHAPTER

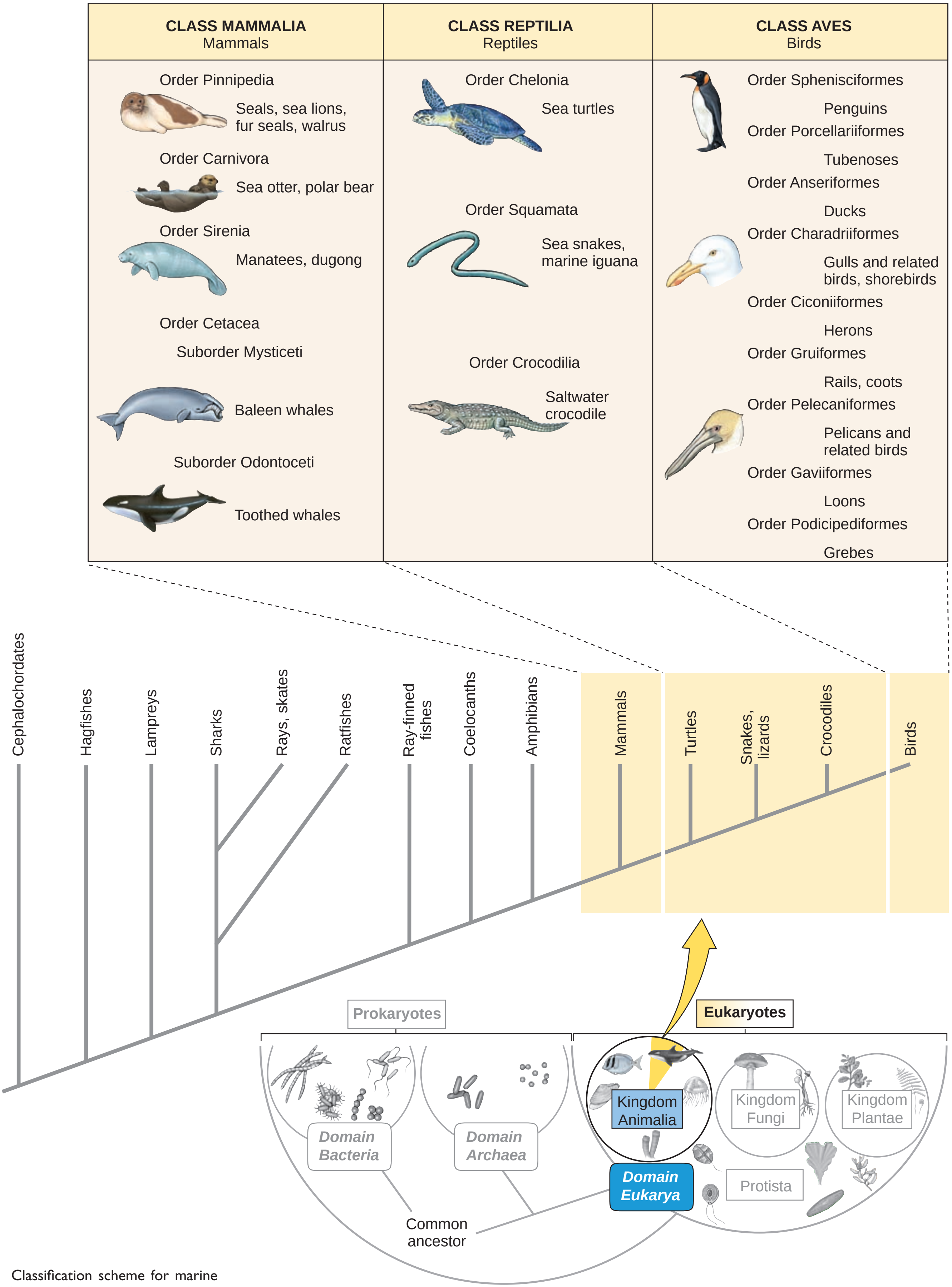
Marine Reptiles, Birds, and Mammals

Vertebrates originated in the ocean and have thrived there ever since. Roughly 350 million years ago, vertebrates invaded the land as well, an event that changed life on earth forever. Descended from bony fishes, land vertebrates had to adapt to the harsher conditions ashore. They lost the structural support that water provides and had to develop ways of crawling or walking to get around. They evolved from fish-like vertebrates with two pairs of limbs as an adaptation for "walking" on the bottom or on land between pools of water (see "When Fishes Stepped on Land," p. 80). Because of this, land-dwelling vertebrates—even snakes—are called **tetrapods,** meaning "four-footed."

Living on land also means having to breathe air. Tetrapods evolved from fishes that had **lungs,** internal air sacs that allow absorption of oxygen directly from air. Tetrapods had to evolve ways to keep from drying out. The delicate egg is especially vulnerable, and the first land tetrapods, the **amphibians** (class **Amphibia**), never really solved this problem. Represented today by frogs, salamanders, and their relatives, amphibians must keep themselves moist, and most lay their eggs in water. None of them are strictly marine.

Other groups of tetrapods solved the problem of water loss and truly adapted to life on land. **Reptiles** (class **Reptilia;** Fig. 9.1) evolved from now-extinct amphibians and for a long time were the dominant land vertebrates. The **birds** (class **Aves**) and **mammals** (class **Mammalia**) both evolved from different groups of now-extinct reptiles.

Having adapted to the land, various groups of reptiles, birds, and mammals turned around and reinvaded the ocean. This chapter deals with these marine tetrapods. Some, like sea



CLASS MAMMALIA Mammals	**CLASS REPTILIA** Reptiles	**CLASS AVES** Birds
Order Pinnipedia Seals, sea lions, fur seals, walrus Order Carnivora Sea otter, polar bear Order Sirenia Manatees, dugong Order Cetacea Suborder Mysticeti Baleen whales Suborder Odontoceti Toothed whales	Order Chelonia Sea turtles Order Squamata Sea snakes, marine iguana Order Crocodilia Saltwater crocodile	Order Sphenisciformes Penguins Order Porcellariiformes Tubenoses Order Anseriformes Ducks Order Charadriiformes Gulls and related birds, shorebirds Order Ciconiiformes Herons Order Gruiformes Rails, coots Order Pelecaniformes Pelicans and related birds Order Gaviiformes Loons Order Podicipediformes Grebes

Cephalochordates
Hagfishes
Lampreys
Sharks
Rays, skates
Ratfishes
Ray-finned fishes
Coelocanths
Amphibians
Mammals
Turtles
Snakes, lizards
Crocodiles
Birds
Prokaryotes
Eukaryotes
Domain Bacteria
Domain Archaea
Kingdom Animalia
Kingdom Fungi
Kingdom Plantae
Protista
Domain Eukarya
Common ancestor

FIGURE 9.1 Classification scheme for marine reptiles, birds, and mammals.

turtles, have not fully made the transition and still return to land to lay their eggs. Others, like whales, spend their entire lives at sea. They have adapted so completely to a marine existence that their streamlined bodies look almost fish-like. This fish-like appearance, however, belies the fact that they evolved from animals that once, about 55 million years ago, walked on land (see “The Whales That Walked to Sea,” p. 192). Their embryos even have the four limbs that characterize all land vertebrates (see Fig. 9.16).

The marine animals to be covered in this chapter include some of the most fascinating and awesome creatures on the planet. Unfortunately, many are in danger of disappearing forever because of our own greed. Some already have become extinct.

MARINE REPTILES

There are around 7,000 living species of reptiles, including lizards, snakes, turtles, and crocodiles. Their dry skin is covered with scales to prevent water loss. Their eggs have a leathery shell that prevents them from drying out, so reptiles can lay their eggs on land. Like most fishes, reptiles are **poikilotherms** and **ectotherms,** commonly called “cold-blooded.” Like other poikilotherms, their metabolic rate—and therefore activity level—varies with temperature: they get sluggish in the cold. This tends to keep them out of cold regions, especially on land because the air temperature fluctuates more widely than does the ocean temperature.

Poikilotherms Organisms that have a body temperature that varies with that of the environment.
Ectotherms Organisms that lose metabolic heat to the environment without it affecting their body temperature.
- Chapter 4, p. 75

Reptiles are air-breathing, ectothermic (“cold-blooded”), poikilothermic vertebrates. Their skin is covered with dry scales, and nearly all lay their eggs on land.

Reptiles first appeared more than 300 million years ago, and several different groups have invaded the seas. Many are long gone, like the ichthyosaurs (see Fig. 9.14) that thrived during the so-called Age of Reptiles. Only a few reptiles still roam the seas. Some are rare and endangered; others, however, are common and widely distributed.

Sea Turtles

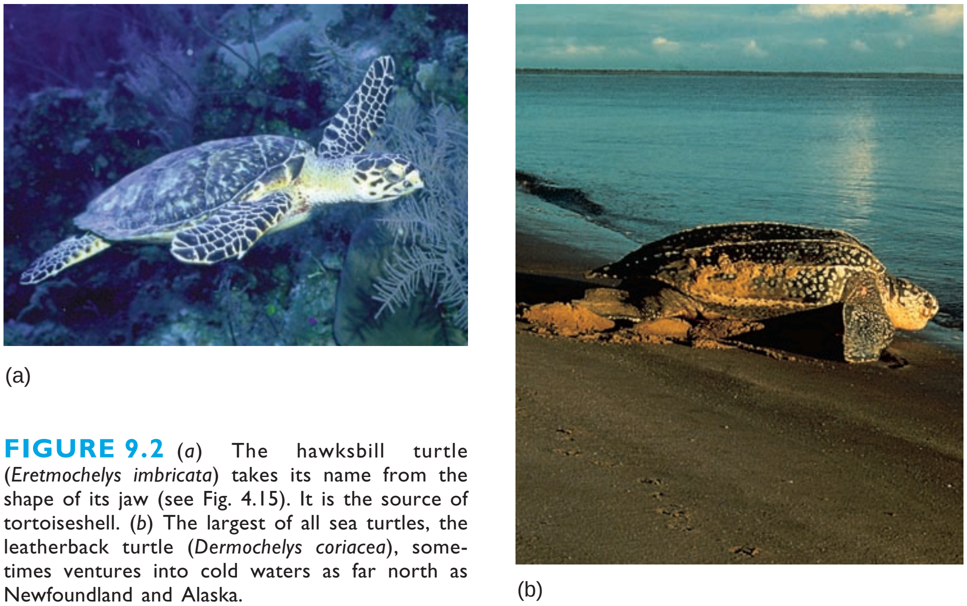
Sea turtles belong to an ancient group of reptiles. Their bodies are enclosed by an armor-like shell, or carapace, that is fused to the backbone (see Table 9.3, p. 209). Unlike land tortoises and turtles, sea turtles cannot retract their heads into the shell. Their legs, particularly the larger forelimbs, are modified into flippers for swimming.

There are only seven species of sea turtles (though some biologists recognize eight), which live primarily in warm waters. Green turtles (*Chelonia mydas,* see photo on p. 180) were once found in coastal waters throughout the tropics. Their shells may grow to 1 m (40 in) in length. They feed mostly on seagrasses and seaweeds. Like all turtles, green turtles lack teeth, but they have strong biting jaws. The hawksbill turtle (*Eretmochelys imbricata;* Fig. 9.2*a*) is smaller, and the shell is reddish brown with yellow streaks. It uses its beak-like mouth to feed on encrusting animals (sponges, sea squirts, barnacles) and seaweeds.

The largest sea turtle is the leatherback (*Dermochelys coriacea;* Fig. 9.2*b*). Individuals may attain a length of 2 m (7 ft) and weigh at least 540 kg (1,200 lb). Instead of a solid shell, they have a series of small bones buried in the dark skin, forming distinct longitudinal ridges. Leatherbacks are an open-water species, the widest ranging of all marine reptiles, and are rarely seen except on nesting beaches. They are deep divers—one individual was tracked diving to 640 m (2,100 ft). Their diet consists largely of jellyfishes. Like other species of sea turtles, leatherbacks are in danger of disappearing forever (see “The Endangered Sea Turtles,” p. 180).

The remaining species of sea turtles have diverse diets, feeding on soft, bottom invertebrates like sponges, soft corals, and jellyfishes as well as hardier invertebrates like crabs and molluscs. The jaws of most species of are adapted for crushing. The leatherback jaws, however, are scissor-like and are used to capture jellyfishes.

All sea turtles must return to land to reproduce. They migrate long distances to lay their eggs on remote sandy beaches, and they were doing so millions of years before humans appeared on the scene. Green turtles still gather to nest on beaches on the east coast of Central America, Northern Australia, Southeast



(a)

(b)

FIGURE 9.2 (*a*) The hawksbill turtle (*Eretmochelys imbricata*) takes its name from the shape of its jaw (see Fig. 4.15). It is the source of tortoiseshell. (*b*) The largest of all sea turtles, the leatherback turtle (*Dermochelys coriacea*), sometimes ventures into cold waters as far north as Newfoundland and Alaska.

The Endangered Sea Turtles

Humans are by far the most formidable and destructive enemies of sea turtles. Sea turtles can live for months without food or water. In the days before refrigeration, sailors kept them alive aboard ship as a source of fresh meat, storing them on their backs for months. Coming ashore by the thousands, females were an easy catch. They were, and still are, immobilized by turning them on their backs to be gathered later without giving them a chance to lay their eggs. The green turtle is especially esteemed for its meat, and its cartilage is used to make turtle soup. An estimated 35,000 green and loggerhead (*Caretta caretta*) turtles are illegally killed annually in northwestern Mexico. Some people consider the oily leatherback meat a delicacy.

The polished shell of the hawksbill is the source of valuable **tortoiseshell** used to make jewelry, combs, and other articles (see Fig. 18.15), particularly in Japan. Sea turtle leather, which is soft and durable, is much prized for shoes, handbags, and wallets. Leather articles from illegally slaughtered animals still make their way into the United States from Mexico and other countries. The oil of many sea turtles is also of commercial value. Even baby sea turtles are valuable. They are stuffed and sold as souvenirs.

Many nesting areas have been turned into resorts or public beaches. Females searching for nesting beaches avoid lights because dark areas along the horizon indicate land, and lights along a beach look like a starry horizon. Artificial lighting also disorients baby turtles after hatching, so they do not head to sea and therefore die. Turtles drown in fishing nets and choke to death after swallowing plastic bags they think are jellyfishes. Turtle eggs are taken by the bucketful and are located by pushing a stick into the sand until it comes out yellow. The eggs are eaten or fed to pigs or cattle. Turtle eggs, particularly those of leatherbacks, are said to be an aphrodisiac, a myth that probably arose because adult turtles can be seen copulating for long periods at sea.

The green turtle, once very common, disappeared in many areas as the result of relentless overexploitation for eggs and meat. Its numbers, however, have been increasing in many areas, undoubtedly the result of protection. It is the most widely distributed and most common of all sea turtles.

All sea turtle species are classified as **threatened** worldwide because their numbers are low (see Table 18.1, p. 416). Only about 4,000 nesting leatherback turtles remain in the Pacific Ocean. Sea turtles are not protected at all in many countries and, in those where they are, enforcement is difficult. Shrimp nets are estimated to kill up to 4,000 sea turtles a year in Southeast Asia. Many more become entangled in gill and drift nets and die asphyxiated. It is impossible to protect all coasts and nesting grounds from fishers and egg hunters. Stricter worldwide enforcement of conservation practices, the control of pollution, the regulation of trade in sea turtle products, and the restocking of former nesting areas might help save them.

Green turtle (*Chelonia mydas*).

All six species of sea turtles in the United States are protected under the Endangered Species Act of 1973. Three of these species are classified as threatened. Three other species are classified as **endangered** and in great danger of disappearing: the leatherback, hawksbill, and Kemp's (or Atlantic) ridley (*Lepidochelys kempii*). The number of leatherbacks has decreased by 95% since the early 1980s, mostly victims of longline fishing. Shrimp nets in the Gulf of Mexico have been especially deadly to the Kemp's ridley turtle, once very common but now so rare that only a few hundred breeding females remain. It is the most endangered of all sea turtles. For some time, shrimp nets in the United States have been fitted with turtle exclusion devices, or TEDs, that allow sea turtles to escape once caught in the nets.

Asia, Ascension Island (in the middle of the South Atlantic), and a few other locations. Marine biologists have tagged adult sea turtles at Ascension and have found that the turtles regularly cross 2,200 km (1,360 mi) of open water to their feeding grounds along the coast of Brazil (see foldout map at the end of the book), a journey that takes a little more than two months. Though we are still not sure how they find their way, there is evidence that they do it by sensing the earth's magnetic field.

Most of what we know about the reproduction of sea turtles is based on the green turtle. They return to their nesting areas every two to four years, often against prevailing currents. Evidence that females return to the beaches where they were born has been obtained by analyzing the **DNA** of breeding populations at sites around the world. The DNA of turtles breeding in one area differs from the DNA of turtles breeding at other sites. It thus appears that turtles keep returning to the same place generation after generation.

Copulating pairs of sea turtles are often seen offshore, but only females venture ashore, usually at night. Therefore, biologists have mostly tagged females because turtles can be tagged most easily on land. The females congregate on the beach, and each excavates a hole in the sand using both pairs of flippers (Fig. 9.3). They lay between 100 and 160 large, leathery eggs in this nest. The female covers the eggs with sand before she returns to the sea. She may make several trips ashore during the breeding season, laying eggs each time.

The eggs hatch after about 60 days of incubation in the sand. The baby turtles must then dig themselves out of the sand and crawl all the way back to the water, protected by darkness if they're lucky. Green turtles and other sea turtles have many enemies. The eggs are often eaten by dogs, ghost crabs, wild pigs, and other animals. The hatchlings are easy prey for land crabs and birds, especially during the day. Even more young turtles are lost in the water, where they are taken by a variety of fishes and seabirds.

Sea Snakes

Approximately 55 species of **sea snakes** are found in the tropical Indian and Pacific oceans (Fig. 9.4). Their bodies are laterally flattened and the tail paddle-shaped for swimming. Most are

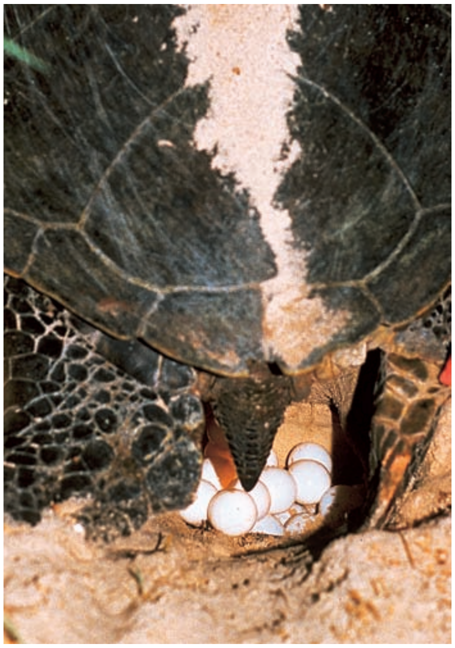


FIGURE 9.3 Egg laying in green turtles (*Chelonia mydas*) culminates a long and hazardous trip by females. It is at this time that they are most vulnerable. This photograph was taken on Sipadan Island, off the northeastern coast of Borneo, Malaysia.

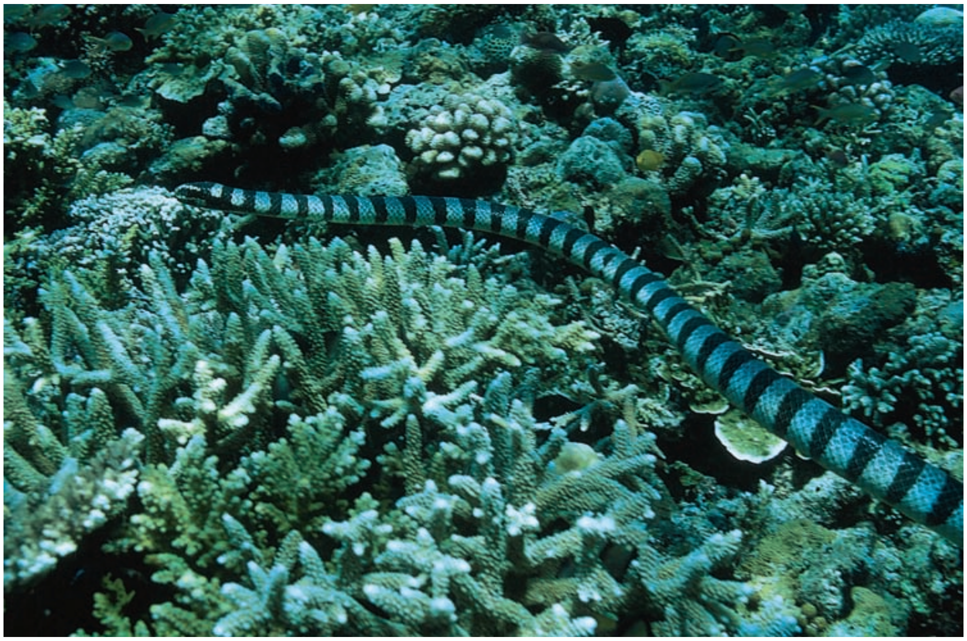


FIGURE 9.4 Sea snakes are found from the Indian Ocean coast of South Africa to the Pacific coast of tropical America, where they occur from the Gulf of California to Ecuador. They sometimes are found under floating debris, feeding on the fish it attracts. The conspicuous coloration of sea snakes may be a warning to potential predators because many fishes learn to associate the bright colors with danger. There are no sea snakes in the Atlantic, but a sea-level canal across Central America may allow their migration into the Caribbean.

1 to 1.3 m (3 to 4 ft) long. Practically all sea snakes lead a totally marine existence. They mate in the ocean and are **ovoviviparous,** giving birth to live young. A few species, however, still come ashore to lay their eggs.

Like all snakes, sea snakes are carnivores. Most feed on bottom fish, a few specializing in fish eggs. They are closely related to cobras and their allies, the most venomous of all snakes. Sea snakes are among the most common of all venomous snakes, and their bites can be fatal to humans. Fortunately, they are rarely aggressive, and the mouth is too small to get a good bite. Most casualties, swimmers accidentally stepping on them and fishers removing them from nets, have been reported in Southeast Asia. Sea snakes are also victims of overexploitation. They are hunted for their skins, and some species have become rare.

DNA A complex *nucleic acid* that contains a cell's genetic information.
- Chapter 4, p. 65

Ovoviviparous Animals Animals in which the eggs develop and hatch in the reproductive tract of females.
- Chapter 8, p. 174

Other Marine Reptiles

An unusual lizard is among the unique inhabitants of the Galápagos Islands, which lie off the Pacific coast of South America. The **marine iguana** (*Amblyrhynchus cristatus;* Fig. 9.5) spends most of its time basking in large groups on rocks along the coast, warming up after swimming in the cold water. It eats seaweeds and can dive as deep as 10 m (33 ft) to graze.

The other marine reptile is the **saltwater crocodile** (*Crocodylus porosus;* see Fig. 17.17), which inhabits mangrove swamps and estuaries in the eastern Indian Ocean, Australia, and some of the western Pacific

FIGURE 9.5 Though rather awkward on land, the marine iguana of the Galápagos Islands (*Amblyrhynchus cristatus*) is an elegant swimmer under water. It swims by undulating the body and the laterally flattened tail, the tip of which is shown on the bottom left.

islands. Saltwater crocodiles live mostly on the coast but also found in rivers and are known to venture into the open sea. There is a record of an individual 10 m (33 ft) long, but they are rarely over 6 m (20 ft). They are among the most aggressive of all marine animals and are known to attack and eat people. Where they occur, they are more feared than sharks.

Marine reptiles include the sea turtles, sea snakes, the marine iguana, and the saltwater crocodile.

SEABIRDS

Birds have some significant advantages over reptiles, including the ability to fly. Birds are **homeotherms,** commonly referred to as "warm-blooded." They are also **endotherms.** This has allowed them to live in a wide variety of environments. Their bodies are covered with waterproof feathers that help conserve body heat. Waterproofing is provided by oil from a gland above the base of the tail. Birds preen by rubbing the oil into their feathers with their beaks. Flight is made easier by their light, hollow bones. Furthermore, their eggs have hard shells that are more resistant to water loss than those of reptiles.

Birds are endothermic ("warm-blooded"), homeothermic vertebrates that have feathers and light bones as adaptations for flight.

Seabirds are birds that spend a significant part of their lives at sea and feed on marine organisms. Most breed in large colonies on land, mate as lifelong pairs, and take care of their young. True seabirds have webbed feet for swimming.

Seabirds have evolved from several different groups of land birds. As a result, they differ widely in their flying skills, feeding mechanisms, and ability to live away from land.

Seabirds are birds that nest on land but feed entirely or partially at sea.

Though comprising only about 3% of the estimated 9,700 species of birds, seabirds are distributed from pole to pole, and their impact on marine life is significant. Most are predators of fish, squid, and bottom invertebrates, but some feed on plankton. Seabirds have amazing appetites. They need a lot of food to supply the energy required to maintain their body temperature.

Penguins

Penguins (Fig. 9.6*a*) are flightless, with wings modified into stubby "flippers" that allow them to "fly" underwater. Their bones are denser than those of other birds to reduce buoyancy and make diving easier.

Penguins are spectacular swimmers, propelling their streamlined bodies with powerful strokes of the wings (see Fig. 9.14). They can also jump out of the water and sometimes cover long distances by alternately swimming and jumping. On land it is another story: they are clumsy and awkward. They are nearsighted, having eyes that are adapted for underwater vision.

Penguins are also adapted for cold temperatures. Protection against low temperatures is provided by a layer of fat under the skin. The dense, waterproof feathers trap air that, warmed by body heat, protects against the cold like a down coat. All but 1 of the 18 species of penguins live primarily in Antarctica and other cold temperate regions of the Southern Hemisphere. The exception is the Galápagos penguin (*Spheniscus mendiculus*), which lives right on the Equator. Even so, this penguin is confined to regions in the Galápagos that are bathed by cold currents.

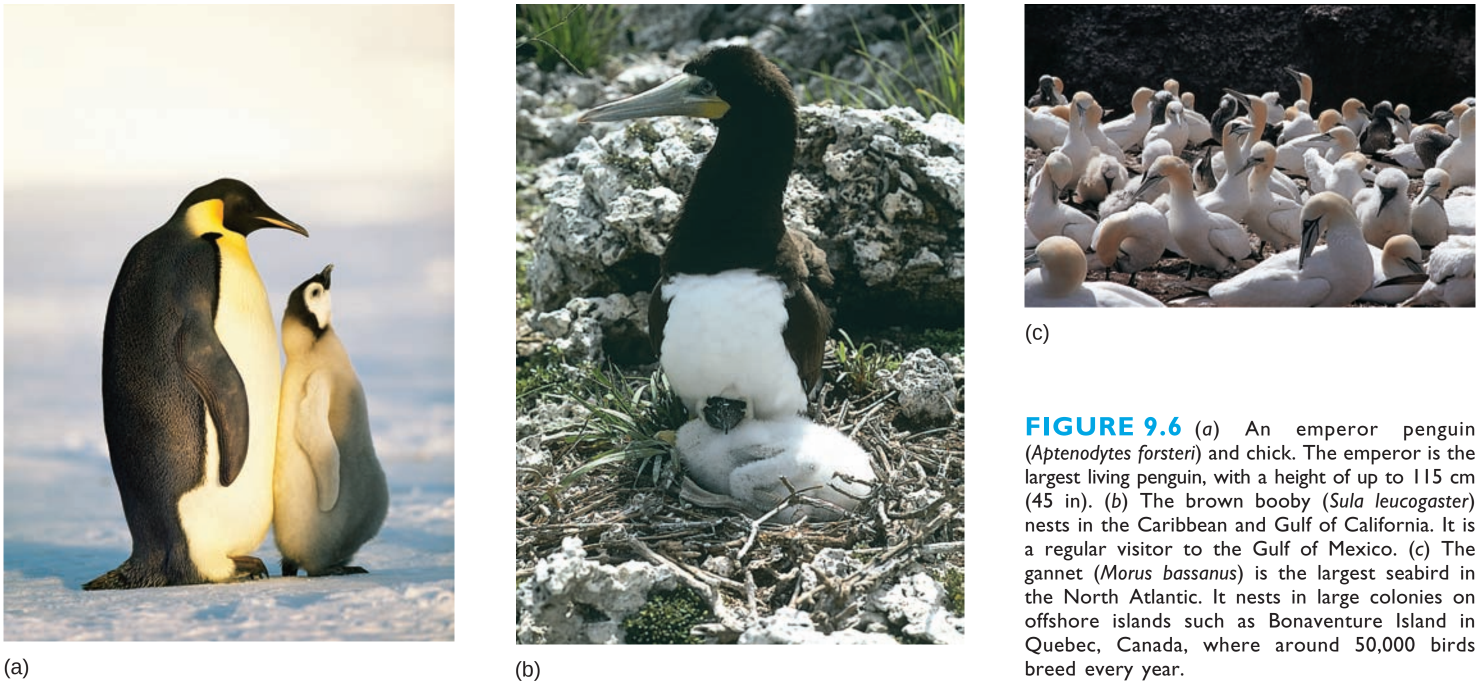

(a) (b) (c)

FIGURE 9.6 (*a*) An emperor penguin (*Aptenodytes forsteri*) and chick. The emperor is the largest living penguin, with a height of up to 115 cm (45 in). (*b*) The brown booby (*Sula leucogaster*) nests in the Caribbean and Gulf of California. It is a regular visitor to the Gulf of Mexico. (*c*) The gannet (*Morus bassanus*) is the largest seabird in the North Atlantic. It nests in large colonies on offshore islands such as Bonaventure Island in Quebec, Canada, where around 50,000 birds breed every year.

The larger penguins, like the imposing emperor penguin (*Aptenodytes forsteri;* Fig. 9.6*a*), hunt for fish and squid. The Adélie (*Pygoscelis adeliae*) and other small penguins feed mostly on **krill.** Penguins have strong beaks, a characteristic of seabirds that feed on fish and large plankton like krill (Fig. 9.7*b*). Some species migrate seasonally between feeding grounds at sea and nesting areas on land or ice. They establish breeding colonies, which in Adélies may number more than a million pairs.

Emperor penguins mate for life. The male incubates a single, large egg during the dark Antarctic winter. The female leaves to feed as soon as she lays the egg. The male, standing on ice, must keep the egg warm by holding it on top of his feet and against his body for 64 days. Males huddle together to protect themselves from the cold and the dreadful winter storms.

You may wonder why the penguins lay their eggs at the coldest time of the year. Reproduction is timed so that the egg hatches during the productive Antarctic summer, when food is most plentiful. When the egg hatches, the female finally returns and regurgitates food for the fuzzy chick. After that, both parents take turns feeding the chick. While the parents feed, the fast-growing young are herded into groups guarded by a few adult "baby-sitters." Returning parents identify their chick among thousands by its voice and appearance. The parents continue to feed the chick for five and a half months, until it is strong enough to feed itself at sea.

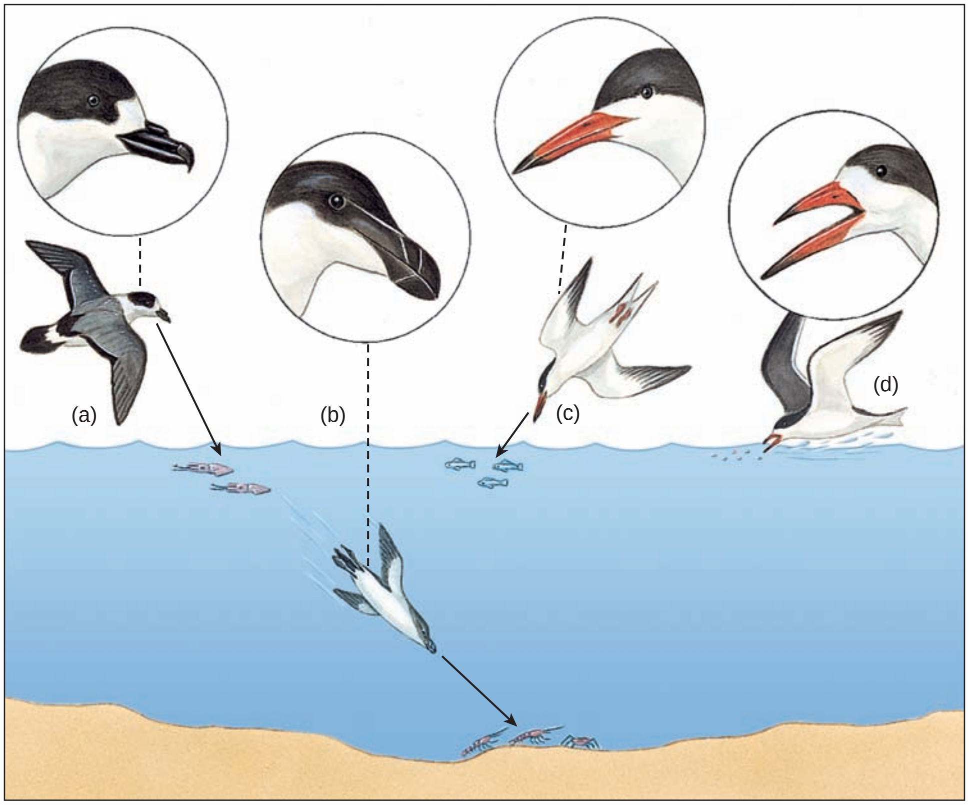


FIGURE 9.7 The shape of a seabird's beak is related to the bird's food and its feeding style. (*a*) In tubenoses like petrels (*Pterodroma*), the beak is relatively short, heavy, and hooked—an ideal shape for holding and tearing prey that is too big to be swallowed whole. Such a beak is best suited for shallow feeding because its size and shape interfere with fast pursuit under water. (*b*) The beak is heavy but more streamlined in the razorbill (*Alca*), penguins (*Aptenodytes* and others), and other seabirds that dive deeper to feed on crustaceans and other prey. (*c*) Terns (*Sterna*), boobies (*Sula*), and other plunge divers have a straight and narrow beak for feeding on fish that are swallowed whole. (*d*) Skimmers (*Rynchops*) are the only birds with a lower beak that is longer than the upper, which permits feeding while flying. Shorebirds that feed on mudflats have a long, thin beak that allows them to get to prey buried in the mud (see Fig. 12.12).

Tubenoses

The **tubenoses** comprise a large group of seabirds with distinctive tube-like nostrils and heavy beaks that are usually curved at the tip (Fig. 9.7*a*). They spend months and even years on the open sea. Like other seabirds and sea turtles, they have **salt glands** that get rid of excess salts; these empty into the nostrils. Tubenoses include the albatrosses (*Diomedea*), shearwaters (*Puffinus*), and petrels (*Pterodroma*).

Tubenoses are very skillful fliers. Most catch fish at the sea surface (Fig. 9.7*a*), though some scavenge on dead birds or whales. The whalebirds, or prions (*Pachyptila*), feed on krill and other plankton. Albatrosses are magnificent gliders with huge wings that hardly ever seem to flap. Wandering albatrosses (*D. exulans*) and royal albatrosses (*D. epomophora*) have wingspans of up to 3.4 m (11 ft), the longest of any bird alive.

Male and female tubenoses remain faithful to each other and perform elaborate courtship and greeting behaviors. Most nest on remote islands, on cliffs that are inaccessible to predators. Incubation and care of the single chick takes eight months, even longer in some species. Tubenoses make some of the most spectacular migrations of any animal. Many breed on islands around Antarctica, then migrate across the open ocean to summer feeding grounds near the Arctic. The wandering albatross gets its name from the fact that it spends two years or more traveling around the Southern Hemisphere before returning to nesting sites near Antarctica. Some non-breeding individuals wander off and pay visits as far away as California and the Mediterranean.

Pelicans and Related Birds

Several quite different-looking seabirds are grouped together because they have webbing between all four toes. They are relatively large fish-eaters of wide distribution.

Homeotherms Organisms able to keep their body temperature more or less constant regardless of the temperature of the environment.
- Chapter 4, p. 76

Endotherms Organisms that retain some metabolic heat, which raises their body temperature.
- Chapter 4, p. 75

Krill Planktonic, shrimp-like crustaceans.
- Chapter 7, p. 136; Figure 17.12

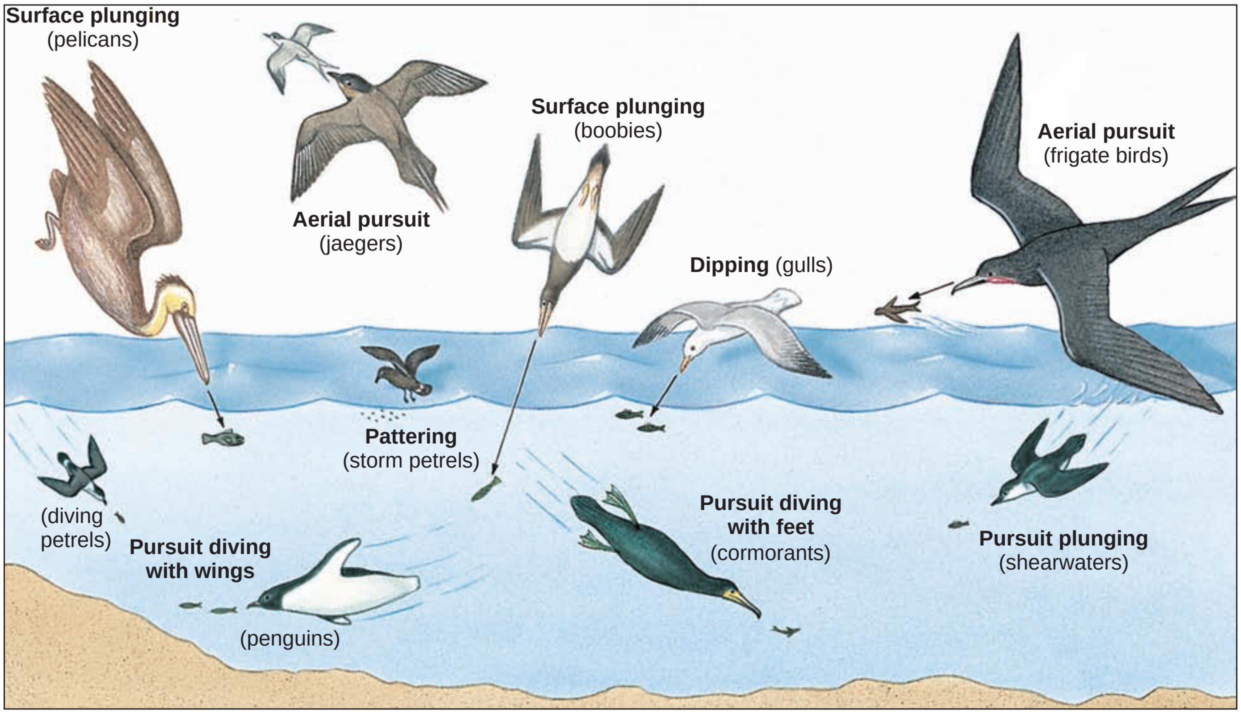

Surface plunging (pelicans)
Aerial pursuit (jaegers)
Surface plunging (boobies)
Aerial pursuit (frigate birds)
Dipping (gulls)
Pattering (storm petrels)
(diving petrels)
Pursuit diving with wings
(penguins)
Pursuit diving with feet (cormorants)
Pursuit plunging (shearwaters)

FIGURE 9.8 Feeding strategies vary widely among seabirds. Pelicans (*Pelecanus*) and boobies (*Sula*) plunge from the air into the water, jaegers (*Stercorarius*) pursue other seabirds and force them to regurgitate food, and frigate birds (*Fregata*) take fish from the surface and steal fish from other seabirds. Gulls (*Larus*) rarely plunge from the air, and storm petrels (*Oceanodroma*) simply flutter over the waves. Divers like cormorants (*Phalacrocorax*) pursue prey under water, swimming with their wings or feet. Mudflat shorebirds also follow various strategies (see Fig. 12.13).

Pelicans (*Pelecanus*) have a unique pouch below their large beaks. Some species, like the brown pelican (*P. occidentalis;* see Fig. 18.9), feed by plunging into the water and catching fish in the pouch (Fig. 9.8). The brown pelican was once common along the coasts of the United States but was decimated by pesticide pollution (see "Persistent Toxic Substances," p. 409). It has made a comeback as a result of restrictions on the manufacture and use of the pesticide DDT. **Cormorants** (*Phalacrocorax*) are black, long-necked seabirds that dive and pursue their prey. They can be easily identified by their low flights over water and the fact that they float low in the water, with only the neck above the surface. **Frigate birds** (*Fregata;* see photo on p. 177) have narrow wings and a long, forked tail. They soar majestically along the coast, forcing other seabirds to regurgitate fish in midair or catching prey from the surface (Fig. 9.8). These agile pirates seldom enter the water, not even to rest, because their feathers are not very waterproof.

Pelicans and related species nest in large colonies along the coast. They build messy nests of twigs and anything else they can find. The excrement of millions of boobies (see Fig. 9.6*b*), cormorants, pelicans, and other seabirds accumulates as **guano.** Guano deposits are particularly thick in dry coastal regions and islands near very productive waters, such as the coasts of Perú, Chile, and southwest Africa. These deposits are mined for fertilizer (see "Of Fish and Seabirds, Fishers and Chickens," p. 389).

Gulls and Related Birds

Gulls (*Larus*) and their kin make up the largest variety of seabirds. Common and widespread, gulls are predators and scavengers happy to eat just about anything (Fig. 9.8). They are very successful in the company of humans and congregate near piers, garbage dumps, or anywhere else we throw refuse. Jaegers (*Stercorarius*) and skuas (*Catharacta*) are gull-like predators that steal fish from other birds (Fig. 9.8). They nest near the rookeries of penguins and other seabirds and eat their eggs and young.

Terns (*Sterna*) are graceful flyers that hover over their prey before plunging for it. Their slender beaks are specialized to catch small fish, which they swallow whole (Fig. 9.7*c*). The Arctic tern (*S. paradisaea*) is another amazing wanderer. It breeds in the Arctic during the northern summer, travels 16,000 km (10,000 mi) to Antarctica for the southern summer, and then returns to the Arctic.

Also related to gulls are several cold-water diving seabirds. Puffins (*Fratercula*) have heavy beaks similar to those of parrots. The related razorbill (*Alca torda*) is a black and white bird reminiscent of penguins (Fig. 9.7*b*). In fact, these birds may fill the role of penguins, which are absent in the Northern Hemisphere. Like penguins, they use their wings to swim under water. Their extinct cousin, the great auk (*Pinguinus impennis*), looked and acted like a penguin. Great auks once lived in great numbers in the North Atlantic but were slaughtered for their eggs, meat, and feathers. The last great auk died in 1844.

Shorebirds

Usually included among the seabirds are many species of wading **shorebirds,** most of which do not have webbed feet. Because they do not swim much, they are not really seabirds in the strict sense. Many live in inland waters as well as the sea. Some are common in estuaries and coastal marshes. Plovers, sandpipers, and similar birds are related to gulls (see Fig. 9.1). Many other shorebirds may live on the coast: rails, coots, herons, egrets, and even ducks. The distribution and significance of shorebirds in estuaries is discussed in Chapter 12.

MARINE MAMMALS

About 200 million years ago another major group of air-breathing vertebrates, the mammals (class Mammalia), evolved from now-extinct reptiles. For a long time the mammals were overshadowed by the dinosaurs, which were reptiles. About 65 million years ago, however, the dinosaurs disappeared. It was then that mammals thrived, taking the place of the dinosaurs. There are now roughly 4,600 species of mammals, including humans. Fishes, reptiles, and birds each outnumber mammals in number of species.

Like birds, mammals have the advantage of being endotherms, or "warm-blooded," and homeotherms. The skin of mammals, however, has hair instead of feathers to retain body heat. With few exceptions, mammals are **viviparous.** The embryo receives nutrients and oxygen through the **placenta,** a membrane that connects it to the womb. It is also known as the afterbirth. The newborn is fed by milk secreted by the mother's **mammary glands.** Instead of releasing millions of eggs, mammals produce few—but well-cared-for—young.

And then there is the brain. It is larger in relation to body size and far more complex than that of other vertebrates, allowing the storage and processing of more information. This accounts in part for the amazing adaptability of mammals. They live anywhere there is air to breathe and food to eat. This, of course, includes the ocean.

At least five different groups of land mammals succeeded in invading the oceans. They have followed different paths in adapting to the marine environment. Some are so fish-like that we have to remind ourselves that they have hair and bear live young nourished by their mother's milk.

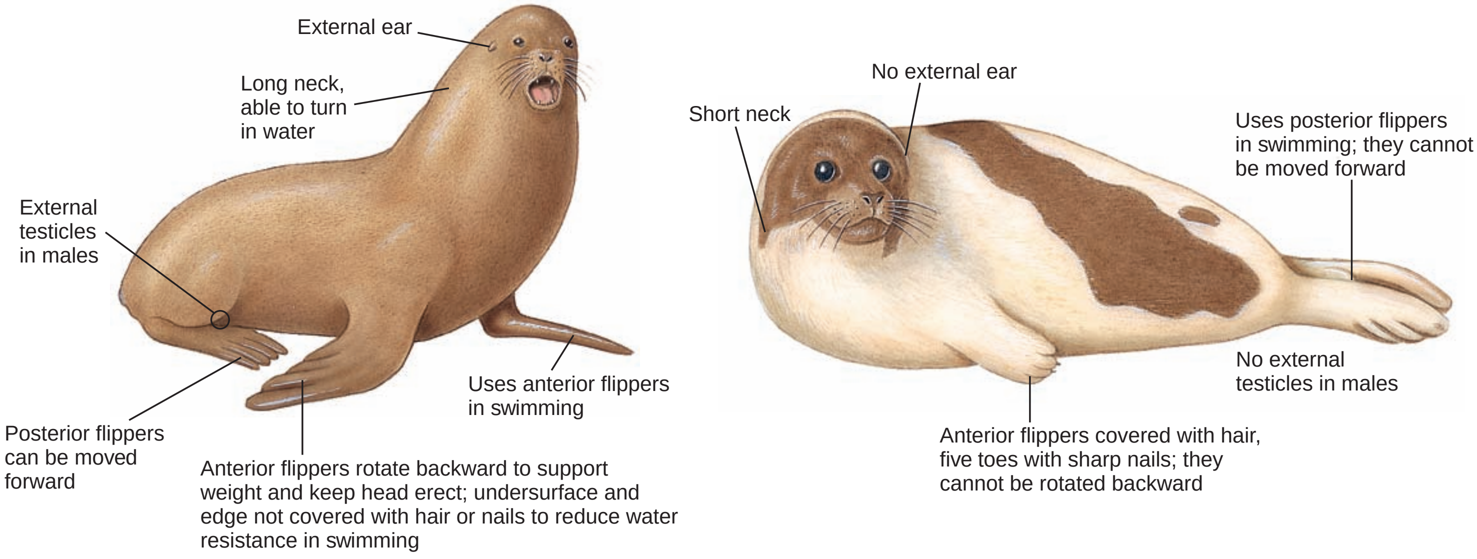
Seals, Sea Lions, and the Walrus

Seals and related forms are marine mammals that have paddle-shaped flippers for swimming but still need to rest and breed on land. They make up one of the 19 or 20 major groups, or orders, of mammals, the **pinnipeds** (order **Pinnipedia;** see Fig. 9.1). Pinnipeds evolved from an early form of terrestrial carnivore (order Carnivora), which includes cats, dogs, bears, and their kin. The similarities are so close that many biologists classify them with the carnivores. Pinnipeds are predators, feeding mostly on fish and squid. Their streamlined bodies are adapted for swimming (Fig. 9.9).

Most pinnipeds live in cold water. To keep warm they have a thick layer of fat, called **blubber,** under their skin. Besides acting as insulation, it serves as a food reserve and helps provide buoyancy. Some pinnipeds also have bristly hair for added protection against the cold. Many of them are quite large, which also helps conserve body heat because large animals have less surface area for their size than small animals and therefore lose less body heat (see Fig. 4.17).

Pinnipeds, which include seals and their relatives, are marine mammals, with flippers and blubber, that need to breed on land.

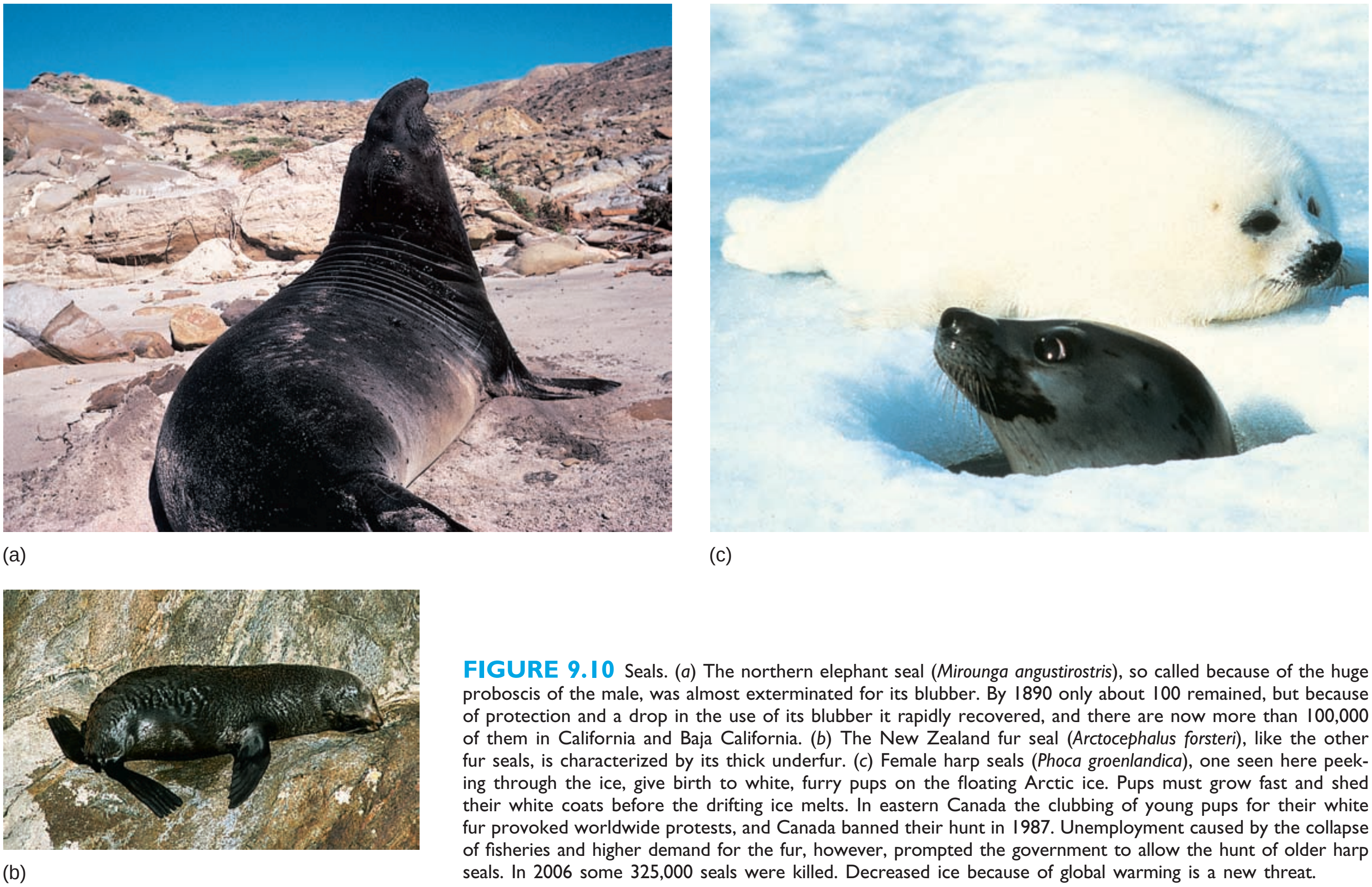
Viviparous Animals Live-bearing animals whose embryos develop within their mothers' bodies and are nourished by the maternal bloodstream.
- Chapter 8, p. 174


External ear
Long neck, able to turn in water
External testicles in males
Posterior flippers can be moved forward
Anterior flippers rotate backward to support weight and keep head erect; undersurface and edge not covered with hair or nails to reduce water resistance in swimming
Uses anterior flippers in swimming
No external ear
Short neck
Uses posterior flippers in swimming; they cannot be moved forward
No external testicles in males
Anterior flippers covered with hair, five toes with sharp nails; they cannot be rotated backward

(a) **Sea lions and fur seals**

(b) **Seals**

FIGURE 9.9 Though they differ in some structural features and the ways in which they swim and move on land, (*a*) sea lions and fur seals and (*b*) seals are now thought to have evolved from the same group of land carnivores.



(a) (c) (b)

FIGURE 9.10 Seals. (*a*) The northern elephant seal (*Mirounga angustirostris*), so called because of the huge proboscis of the male, was almost exterminated for its blubber. By 1890 only about 100 remained, but because of protection and a drop in the use of its blubber it rapidly recovered, and there are now more than 100,000 of them in California and Baja California. (*b*) The New Zealand fur seal (*Arctocephalus forsteri*), like the other fur seals, is characterized by its thick underfur. (*c*) Female harp seals (*Phoca groenlandica*), one seen here peeking through the ice, give birth to white, furry pups on the floating Arctic ice. Pups must grow fast and shed their white coats before the drifting ice melts. In eastern Canada the clubbing of young pups for their white fur provoked worldwide protests, and Canada banned their hunt in 1987. Unemployment caused by the collapse of fisheries and higher demand for the fur, however, prompted the government to allow the hunt of older harp seals. In 2006 some 325,000 seals were killed. Decreased ice because of global warming is a new threat.

The largest group of pinnipeds, including some 19 species, is the seals. Seals are distinguished by having rear flippers that cannot be moved forward (Fig. 9.9*b*). On land they must move by pulling themselves along with their front flippers. They swim with powerful strokes of the rear flippers.

Harbor seals (*Phoca vitulina;* Fig. 9.9*b*) are common in both the North Atlantic and North Pacific. Elephant seals (*Mirounga;* Fig. 9.10*a*) are the largest pinnipeds. Males, or bulls, reach 6 m (20 ft) in length and can weigh as much as 3,600 kg (4 tons). One unusual seal is the crabeater seal (*Lobodon carcinophagus*), which feeds on Antarctic krill. These seals strain krill from the water with their intricately cusped, sieve-like teeth. Unlike most seals, monk seals (*Monachus*) live in warm regions. The Mediterranean (*M. monachus*) and Hawaiian (*M. schauinslandi*) monk seals are now endangered. A third species, the Caribbean monk seal (*M. tropicalis*), was last seen in 1952.

Seals have been hunted for their skin and meat and for the oil extracted from their blubber. The Marine Mammal Protection Act of 1972 extends protection to all marine mammals and restricts the sale of their products in the United States. For some seals, however, this protection has not been enough (see Table 18.1, p. 416).

Sea lions, or eared seals, and the related **fur seals** are similar to seals except that they have external ears (Fig. 9.9*a*). They can also move their rear flippers forward, so they can use all four limbs to walk or run on land. The front flippers can be rotated backward to support the body, permitting the animal to sit on land with its neck and head raised. Sea lions are graceful and agile swimmers, relying mostly on their broad front flippers. Adult males are much bigger than females, or cows, and have a massive head with a hairy mane (see Fig. 9.32*a*).

There are six species of sea lions and nine of fur seals. The most familiar of all is the California sea lion (*Zalophus californianus;* see Fig. 9.33) of the Pacific coast of North America. These sea lions are the trained barking circus "seals" that do tricks for a fish or two. Fur seals (Fig. 9.10*b*), like the northern fur seal (*Callorhinus ursinus*), were once almost exterminated for their thick fur. Now most are protected around the world, though some species are still hunted. Sea lions are luckier because they lack the underfur of their cousins. Still, both sea lions and fur seals may run afoul of fishers. They sometimes drown in nets or are shot because of their notorious ability to steal fish. Populations of the Steller sea lion (*Eumetropias jubatus*) in Alaska have decreased by 80% since the 1970s, most probably because of a decline in the fish they eat as a result of an increase in commercial fishing. Some blame diseases.

The **walrus** (*Odobenus rosmarus;* Fig. 9.11) is a large pinniped with a pair of distinctive tusks protruding down from the mouth. It feeds mostly on bottom invertebrates, particularly clams. It was once thought that the walrus used its tusks to dig up food, but there is no evidence for this. Instead, these pinnipeds apparently suck up their food as they move along the bottom. The stiff whiskers of the snout probably act as feelers. The tusks are used for defense and to hold or anchor to ice.

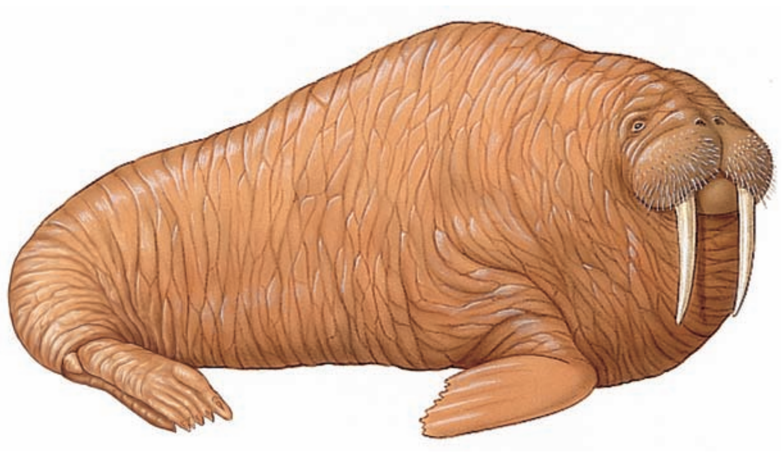


FIGURE 9.11 Walruses (*Odobenus rosmarus*) typically inhabit the edge of pack ice in the Arctic. They migrate as far south as the Aleutian Islands and Hudson Bay, Canada. They also crowd onto beaches on isolated islands that they use as resting places. The walrus is still hunted legally by native Alaskans and Siberians.

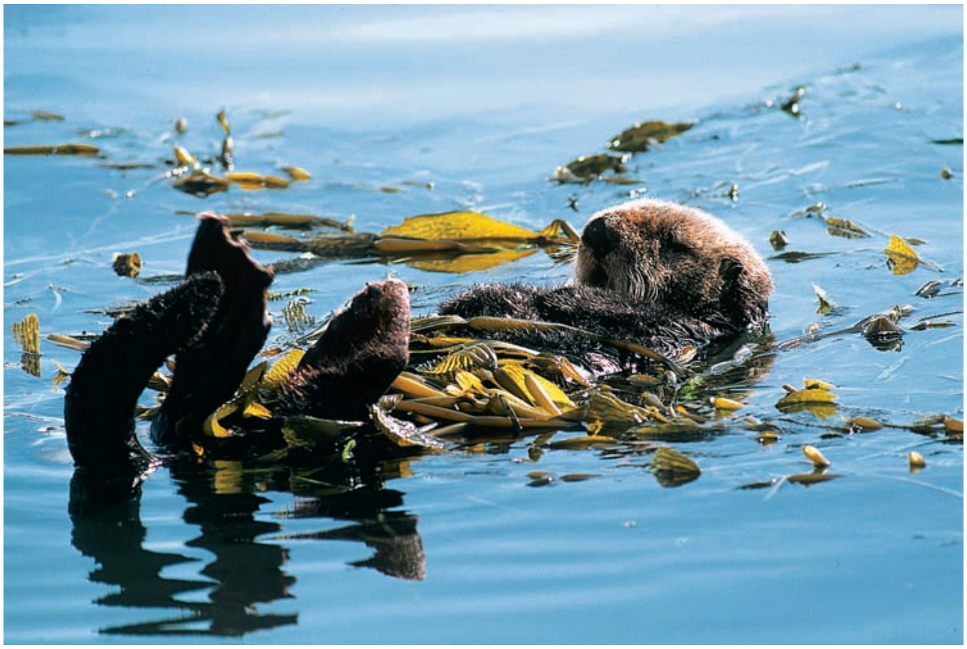


FIGURE 9.12 Sea otters (*Enhydra lutris*) are remarkable for their use of a tool—a rock for crushing sea urchins and molluscs. They carry a flat rock in side "pockets" of loose skin and fur. The sea otter floats on its back at the surface, places the rock on its chest, and crushes its toughest prey against it. Some have been observed carrying and using beer bottles as tools!

Sea Otter and Polar Bear

Though there is doubt about the pinnipeds, the **sea otter** (*Enhydra lutris;* Fig. 9.12) is definitely a member of the order **Carnivora.** The sea otter is the smallest marine mammal; an average male weighs 25 to 35 kg (60 to 80 lb). It also differs from other marine mammals in lacking a layer of blubber. Insulation from the cold is provided by air trapped in its dense fur. This splendid, dark brown fur, unfortunately, attracted hunters. Sea otters were slaughtered to near extinction until they became protected by an international agreement in 1911. The sea otter was then able to slowly expand from the few individuals that had managed to survive in some remote locations. Their numbers, however, have been declining in recent years, particularly in the Aleutian Islands. In California they have slightly declined since peaking in 2004, mostly as a result of disease. The sea otter is still a threatened species (see Table 18.1, p. 416).

Sea otters are playful and intelligent animals. They spend most or all of their time in the water, including breeding and giving birth. The furry pup is constantly groomed and nursed by its mother. Sea otters need to eat 25 to 30% of their body weight per day, so they spend a lot of time looking for food. They satisfy their ravenous appetites with sea urchins, abalone, mussels, crabs, other invertebrates, and even fishes. They live in or around kelp beds from the Pacific coast of Siberia to central California. Sea otters help protect kelp beds from sea urchins (see "Kelp Communities," p. 296).

The **polar bear** (*Ursus maritimus*) is the second member of the order Carnivora that inhabits the marine environment. Polar bears are semiaquatic animals that spend a good part of their lives on drifting ice in the Arctic. They feed primarily on seals, which they stalk and capture as the seals surface to breathe or rest.

Manatees and Dugong

It is hard to believe that relatives of the elephant live at sea. **Manatees** and the **dugong** are also known as **sea cows,** or **sirenians** (order **Sirenia**). They have a pair of front flippers but no rear limbs (Fig. 9.13). They swim with up-and-down strokes of their paddle-shaped, horizontal tail. The round, tapered body is well padded with blubber. They have wrinkled skin with a few scattered hairs. The group is named after the mythical mermaids or sirens whose songs drove sailors crazy!

Sirenians are gentle creatures. They usually live in groups. They are the only strict vegetarians among marine mammals. Their large lips are used to feed on seagrasses and other aquatic vegetation. All sirenians are large. Dugongs may reach 3 m (10 ft) and 420 kg (930 lb), manatees 4.5 m (almost 15 ft) and 600 kg (1,320 lb). The largest sirenian of all was the now-extinct Steller's sea cow, which supposedly grew to 7.5 m (25 ft) long (see Fig. 18.13).

Humans have exploited sirenians for their meat (which supposedly tastes like veal), skin, and oil-rich blubber. Like elephants and other large mammals, they reproduce slowly, typically one calf every three years. Seagrass beds, their source of food, are being destroyed at an alarming rate by anchor and boat damage and by excess silt and nutrients from land, which often results from deforestation and intensive farming. Only four species remain, and all are in danger of extinction (see Table 18.1, p. 416). Three species of manatee (*Trichechus*) live in the Atlantic Ocean;

one is restricted to the Amazon and the others inhabit shallow coastal waters and rivers from Florida to West Africa. The dugong (*Dugong dugon*) is strictly marine and survives from East Africa to some of the western Pacific islands. Its numbers are critically low throughout most of its range.

Whales, Dolphins, and Porpoises

The largest group of marine mammals is the **cetaceans** (order **Cetacea**)—the **whales, dolphins,** and **porpoises.** No group of marine animals has captured our imaginations like the dolphins and whales. They have inspired countless legends and works of art and literature (see "Oceans and Cultures," p. 423). The rescue of whales stranded on a beach or the birth of a killer whale in an oceanarium brings out strong emotions in all of us.

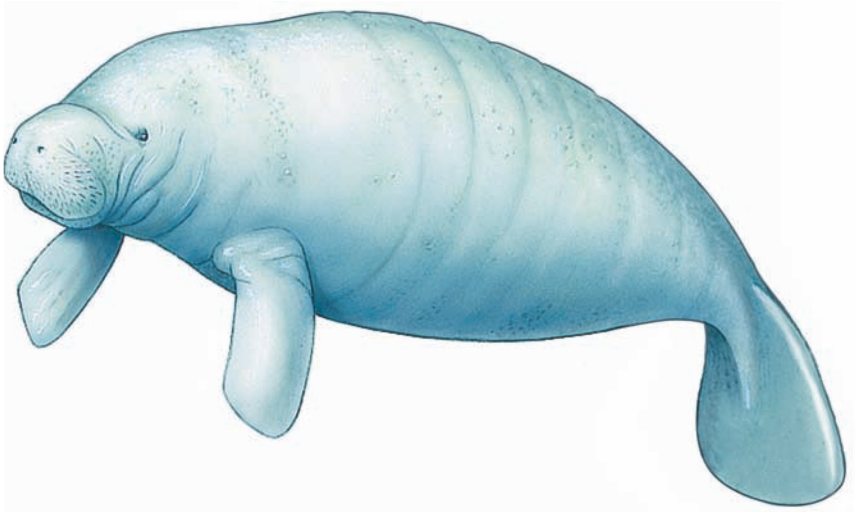


FIGURE 9.13 Only slightly over 3,000 West Indian manatees (*Trichechus manatus*) remain along the coasts and rivers of Florida. Some concentrate in the warm-water effluents of power plants. They are strictly protected, but collisions with boats take their toll. Manatees have been considered as a possible way to control weeds that sometimes block waterways.

Of all marine mammals, the cetaceans, together with the sirenians, have made the most complete transition to aquatic life. Whereas most other marine mammals return to land at least part of the time, these two groups spend their entire lives in the water. The bodies of cetaceans are streamlined and look remarkably fish-like (Fig. 9.14). This is a dramatic example of **convergent evolution,** in which different species develop similar structures because they have similar lifestyles. Though they superficially resemble fishes, cetaceans breathe air and will drown if trapped below the surface. They are "warm-blooded," have hair (though scanty), and produce milk for their young.

Cetaceans have a pair of front flippers (Fig. 9.15), but the rear pair of limbs has disappeared. Actually, the rear limbs are present in the embryo but fail to develop (Fig. 9.16). In adults they remain only as small, useless bones. Like fishes, many cetaceans have a dorsal fin, another example of convergent evolution. The muscular tail ends in a pair of fin-like, horizontal **flukes.** Blubber (see Fig. 4.2) provides insulation and buoyancy; body hair is practically absent. Cetacean nostrils differ from those of other mammals. Rather than being on the front of the head, they are on top, forming a single or double opening called the **blowhole** (Fig. 9.15).

There are approximately 90 species of cetaceans. They are all marine except for 5 species of freshwater dolphins. Cetaceans are divided into two groups: the toothless, filter-feeding whales and the toothed, carnivorous whales, a group that includes the dolphins and porpoises.

Baleen Whales The toothless whales are better known as the **baleen whales.** Instead of teeth they have rows of flexible, fibrous plates, named **baleen,** which hang from the upper jaws (Fig. 9.17). Baleen is made

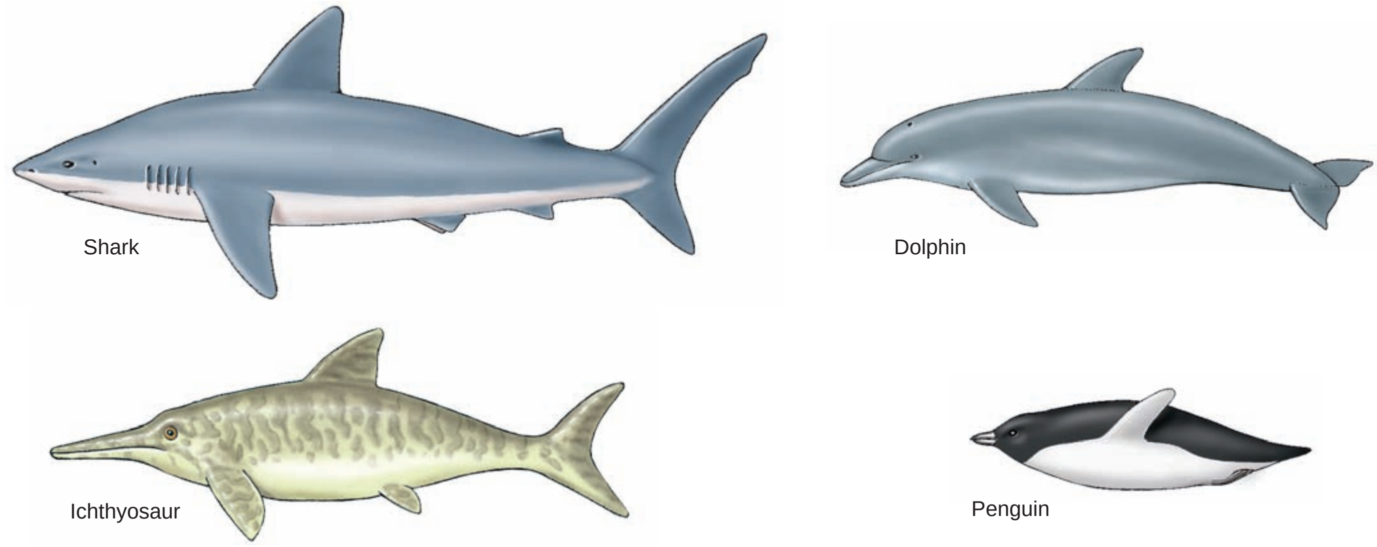


FIGURE 9.14 Streamlining to reduce water resistance evolved independently in different groups of fast-swimming marine animals: sharks, ichthyosaurs (reptiles that became extinct about 65 million years ago), dolphins, and penguins. Notice that dolphins lack posterior fins and that their flukes are horizontal, not vertical like the tail (caudal fin) of fishes (see Fig. 9.24).

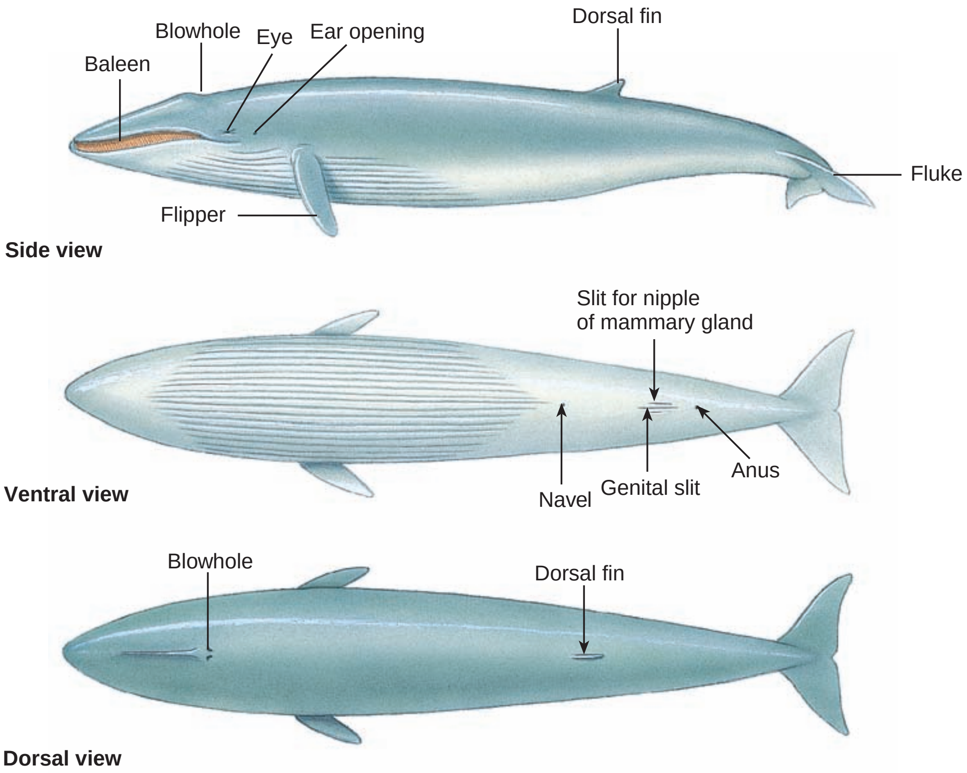

Blowhole
Eye
Ear opening
Dorsal fin
Baleen
Fluke
Flipper
Side view
Slit for nipple of mammary gland
Anus
Navel
Genital slit
Ventral view
Blowhole
Dorsal fin
Dorsal view

FIGURE 9.15 External morphology of a female blue whale (*Balaenoptera musculus*). Males have a genital slit halfway between the anus and navel, and they lack mammary slits.

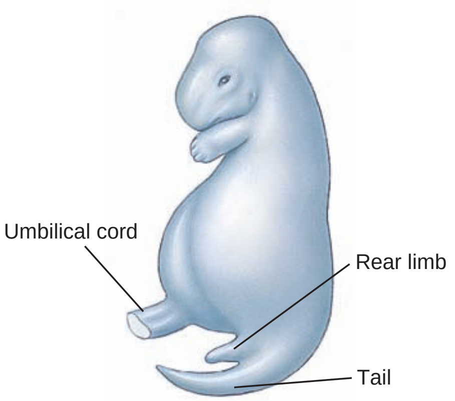

Umbilical cord
Rear limb
Tail

FIGURE 9.16 The fetus of a white-sided dolphin (*Lagenorhynchus*) shows two distinct pairs of limbs; the rear pair will eventually disappear. The umbilical cord connects the fetus with the placenta.

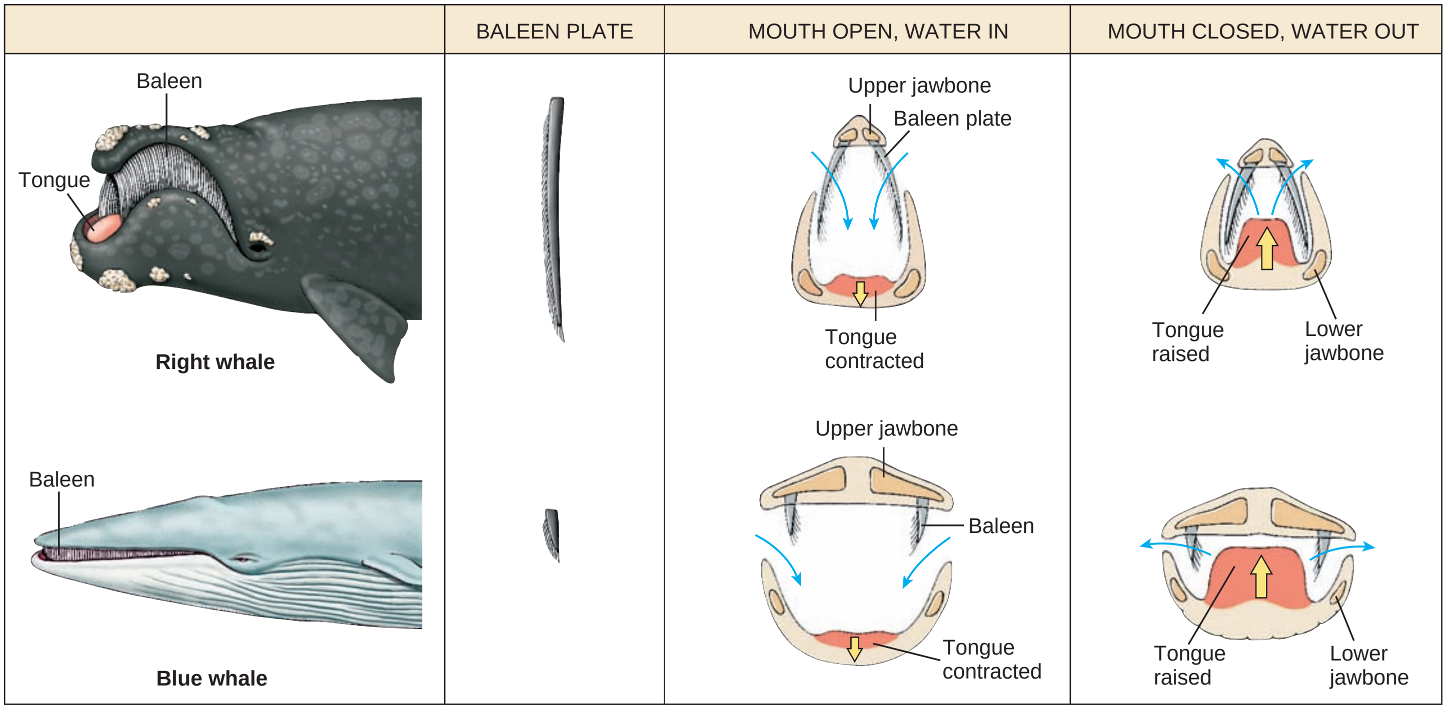

BALEEN PLATE
MOUTH OPEN, WATER IN
MOUTH CLOSED, WATER OUT
Baleen
Tongue
Right whale
Upper jawbone
Baleen plate
Tongue contracted
Tongue raised
Lower jawbone
Baleen
Blue whale
Upper jawbone
Baleen
Tongue contracted
Tongue raised
Lower jawbone

FIGURE 9.17 Filtering in whales involves vertical baleen plates. The number of plates vary with the species, up to an average of 360 on each side in the sei whale (*Balaenoptera borealis*). The plates are up to 3 m (almost 10 ft) in the northern right whale (*Eubalaena glacialis*) but only 1 m (39 in) in the blue whale (*B. musculus*). The baleen, also called whalebone, was once used to make corset stays, backings for billiard tables, and whips. Water is filtered as the mouth closes and the tongue (yellow arrow) pushes up, forcing the water out through the baleen.

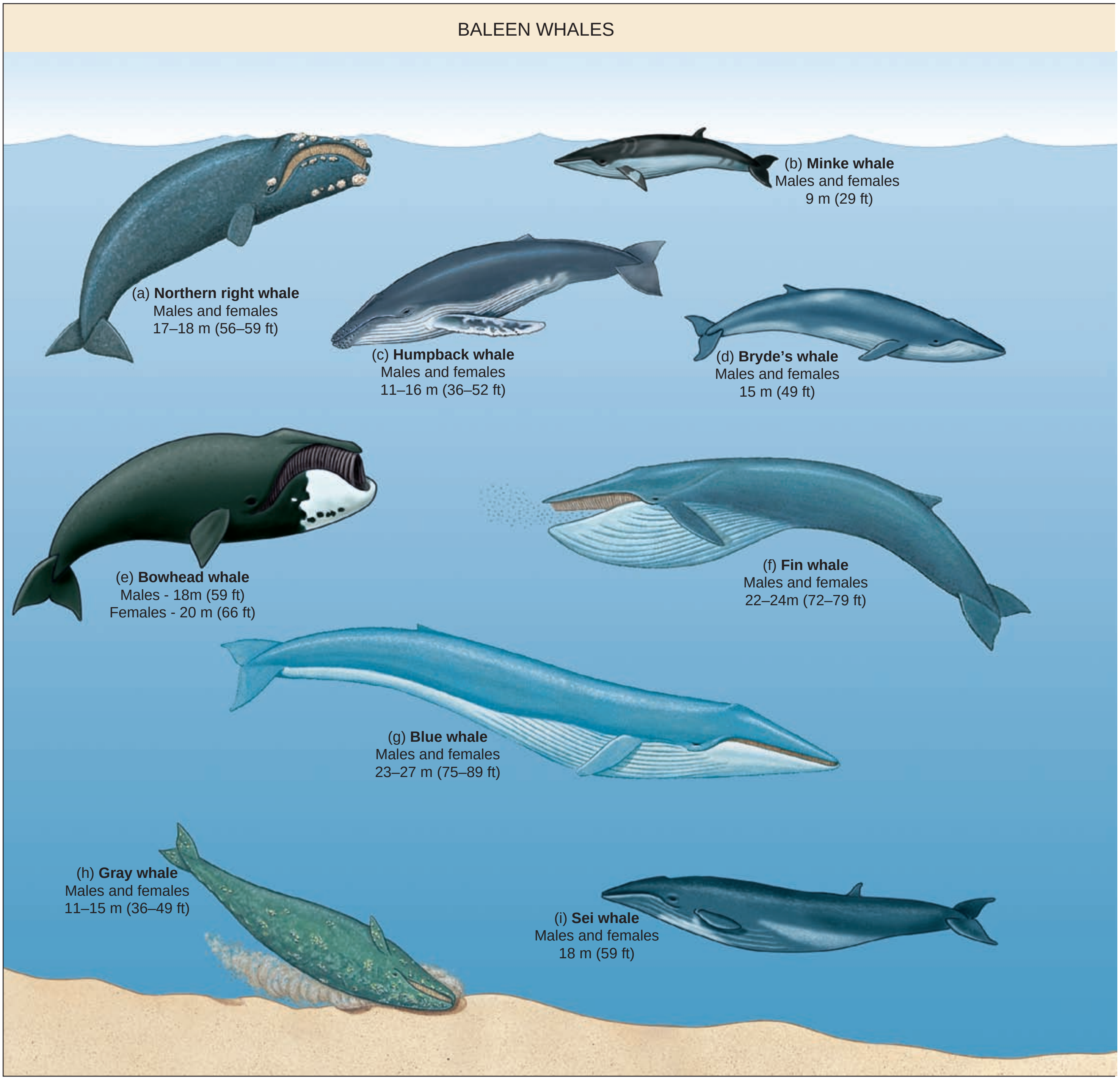
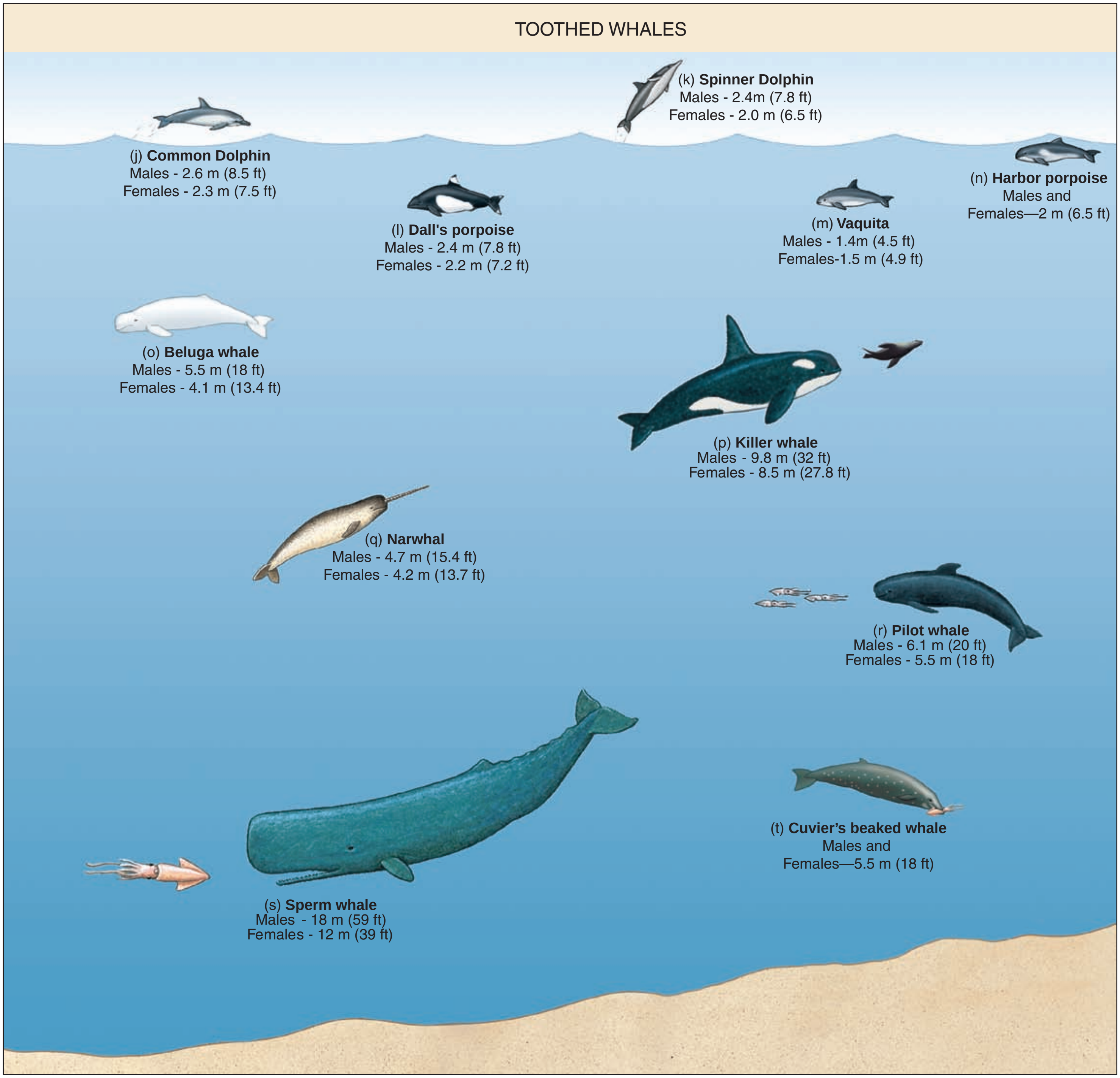

BALEEN WHALES
(a) **Northern right whale**
Males and females
17–18 m (56–59 ft)
(b) **Minke whale**
Males and females
9 m (29 ft)
(c) **Humpback whale**
Males and females
11–16 m (36–52 ft)
(d) **Bryde's whale**
Males and females
15 m (49 ft)
(e) **Bowhead whale**
Males - 18m (59 ft)
Females - 20 m (66 ft)
(f) **Fin whale**
Males and females
22–24m (72–79 ft)
(g) **Blue whale**
Males and females
23–27 m (75–89 ft)
(h) **Gray whale**
Males and females
11–15 m (36–49 ft)
(i) **Sei whale**
Males and females
18 m (59 ft)

FIGURE 9.18 Representative baleen and toothed whales.

of keratin, the same material as our hair and nails. The inner edge of each plate consists of hair-like bristles that overlap and form a dense mat in the roof of the mouth. The whale filter-feeds by taking a big mouthful of water and squeezing it out through the bristles. The whale then licks off the food that is left behind on the bristles and swallows it.

Baleen whales are cetaceans that filter-feed with baleen plates.

Baleen whales are not only the largest whales but also are among the largest animals that have ever lived on earth. There are 13 species of these majestic creatures. They were once common in all the oceans, but overhunting has brought many species to the brink of extinction. The blue whale (*Balaenoptera musculus*), which is actually blue-gray, is the largest of all (Fig. 9.18*g*). Males average 25 m (80 ft), and there is a record of a female 33.5 m (110 ft) long. How do you weigh a blue whale? Very carefully—they average 80,000 to 130,000 kg


TOOTHED WHALES
(j) **Common Dolphin**
Males - 2.6 m (8.5 ft)
Females - 2.3 m (7.5 ft)
(k) **Spinner Dolphin**
Males - 2.4m (7.8 ft)
Females - 2.0 m (6.5 ft)
(l) **Dall's porpoise**
Males - 2.4 m (7.8 ft)
Females - 2.2 m (7.2 ft)
(m) **Vaquita**
Males - 1.4m (4.5 ft)
Females-1.5 m (4.9 ft)
(n) **Harbor porpoise**
Males and
Females—2 m (6.5 ft)
(o) **Beluga whale**
Males - 5.5 m (18 ft)
Females - 4.1 m (13.4 ft)
(p) **Killer whale**
Males - 9.8 m (32 ft)
Females - 8.5 m (27.8 ft)
(q) **Narwhal**
Males - 4.7 m (15.4 ft)
Females - 4.2 m (13.7 ft)
(r) **Pilot whale**
Males - 6.1 m (20 ft)
Females - 5.5 m (18 ft)
(t) **Cuvier's beaked whale**
Males and
Females—5.5 m (18 ft)
(s) **Sperm whale**
Males - 18 m (59 ft)
Females - 12 m (39 ft)

(90 to 140 tons), but the record is an estimated 178,000 kg (200 tons).

The blue whale, the fin whale (*B. physalus;* Fig. 9.18*f*), and the minke whale (*B. acutorostrata;* Fig. 9.18*b*)—together with five other related species—are known as the **rorquals.** Two of these whales were recognized as separate species in 2003. The rorquals and the humpback whale (*Megaptera novaeangliae;* see Figs. 9.18*c* and 9.29), which is often included among the rorquals, feed by gulping up schools of fish and swarms of krill. The lower part of the throat expands when feeding, hence the distinctive, accordion-like grooves on the underside of these whales. Krill is the most important part of the rorqual diet, especially in the Southern Hemisphere. Humpback whales often herd fishes like herring and mackerel by blowing curtains of bubbles around them.

The right whales (*Eubalaena, Caperaea;* Fig. 9.18*a*) and the bowhead whale (*Balaena mysticetus;* Fig. 9.18*e*) feed by swimming along the surface with their huge mouths open. They have the

EVOLUTIONARY PERSPECTIVE

The Whales That Walked to Sea

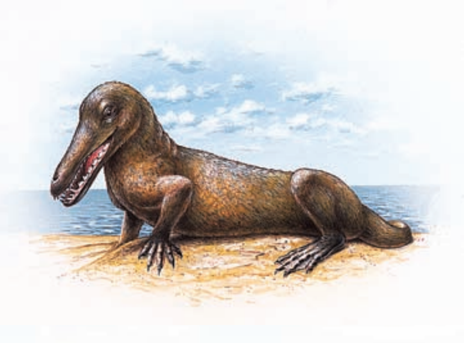
It should be obvious that cetaceans are mammals. Their streamlined bodies, the absence of hind legs, and the presence of a fluke and blowhole cannot disguise their affinities with land-dwelling mammals. Unlike the sea otter and pinnipeds, however, it is not easy to suggest what the first whales looked like and how they evolved into modern cetaceans. Extinct but already fully marine cetaceans are known from the fossil record. How was the gap between a walking mammal and a swimming whale bridged? Missing until recently were fossils clearly intermediate, or transitional, between land mammals and cetaceans.

Very exciting discoveries have finally allowed scientists to reconstruct the most likely origins of cetaceans. It all started in 1979, when a team looking for fossils in north Pakistan found what proved to be the oldest known fossil whale. The fossil was officially described as *Pakicetus* in honor of the country where the discovery was made. *Pakicetus* was found embedded in rocks formed from river deposits that were 52 million years old. The river was actually not far from the shores of the former Tethys Sea (see "Continental Drift and the Changing Oceans," p. 30).

The fossil consists of a complete skull of an **archeocyte,** an extinct group of ancestors of modern cetaceans. Though limited to a skull, the *Pakicetus* fossil provides precious details on the origin of cetaceans. The skull is cetacean-like but its jawbones lack the enlarged space that is filled with fat or oil and used for receiving underwater sound in modern whales (see "Echolocation," p. 200). *Pakicetus* probably detected sound through the ear opening as in land mammals. The skull also lacks a blowhole, another adaptation for diving in cetaceans. Other features, however, show experts that *Pakicetus* is a transitional form between a group of extinct flesh-eating mammals, the mesonychids, and cetaceans. It has been suggested that *Pakicetus* fed on fish in shallow water and was not yet adapted for life in the open ocean. It probably bred and gave birth on land.

Another major discovery was made in Egypt in 1989. Several skeletons of another early whale, *Basilosaurus,* were found in sediments left by the Tethys Sea and now exposed in the Sahara Desert. This whale lived around 40 million years ago, 12 million years after *Pakicetus.* Many incomplete skeletons were found but they included, for the first time in an archeocyte, a complete hind leg that features feet with three tiny toes. The legs are small, far too small to have supported the 50-foot-long *Basilosaurus* on land. *Basilosaurus* was undoubtedly a fully marine whale with possibly non-functional, or **vestigial,** hind legs.

Another remarkable find was reported in 1994, also from Pakistan. The now-extinct whale *Ambulocetus natans* ("the walking whale that swam") lived in the Tethys Sea 49 million years ago. It lived around 3 million years after *Pakicetus* but 9 million years before *Basilosaurus.* The fossil includes a good portion of the hind legs. The legs were strong and ended in long feet very much like those of a modern pinniped. The legs were certainly functional both on land and sea. The whale still retained a tail and lacked a fluke, the major means of locomotion in modern cetaceans. The structure of the backbone shows, however, that *Ambulocetus* swam as modern whales do, by moving the rear portion of its body up and down, even if a fluke was missing. The large hind legs were used for propulsion in water. On land, where it probably bred and gave birth, *Ambulocetus* may have moved around very much as a sea lion does. It was undoubtedly a whale that linked life on land with life at sea.


Ambulocetus natans, the walking whale that swam.

Other fossils found in Pakistan in 2001 link early cetaceans with ungulates, the group that includes animals such as cattle, pigs, and hippos. Some of the oldest bones (at least 50 million years old) were from land-living, wolf-like, hoofed animals. The finding of these fossil whales is one of the most exciting recent discoveries in marine biology. Once an important discovery is made, it spurs new interest, which nearly always leads to more discoveries. Such is the case of the discovery of fossils of a baleen whale that, surprisingly, had teeth. The fossil, found in Australia and described in 2006, clearly belonged to a baleen whale, as evidenced by its skull. The small, big-eyed, 25-million-year-old whale used teeth to capture prey, unlike modern plankton-feeding baleens. Did it use echolocation to find its food, unlike modern baleens? Did it rely only on its large eyes? New discoveries invariably lead to more new questions than answers.

largest baleen plates of the whales but the finest bristles (Fig. 9.17). This allows them to filter small plankton like copepods and some krill (Table 9.1).

Gray whales (*Eschrichtius robustus*) are primarily bottom feeders. When examined, their stomachs contain mostly **amphipods** that inhabit soft bottoms (Table 9.1). Grays stir up the bottom with their pointed snouts and then filter the sediment (Fig. 9.18*b*), leaving characteristic pits on the bottom. Most appear to feed on their right side because the baleen on this side is more worn. Some, however, are "left-handed" and feed on the left side. A 10-week-old female kept in captivity in San Diego, California, ate over 815 kg (1,800 lb) of squid every day, gaining weight at the rate of 1 kg (2.2 lb) an hour.

Toothed Whales The roughly 80 remaining species of cetaceans are toothed whales. Their teeth are adapted for a diet of fish, squid, and other prey. They use the teeth only to catch and hold prey, not to chew it. Food is swallowed whole. As in all cetaceans, food is ground up in one of the three compartments of the stomach. The blowhole has one opening, as opposed to two in the baleen whales.

Table 9.1 Diet of Great Whales

Whale Species	Bottom Invertebrates (%)	Large Zooplankton (%)	Small Squids (%)	Large Squids (%)	Small Pelagic Fishes (%)	Mesopelagic Fishes* (%)	Miscellaneous Fishes (%)
Blue	—	100	—	—	—	—	—
Bowhead	20	80	—	—	—	—	—
Bryde's	—	40	—	—	20	20	20
Fin	—	80	5	—	5	5	5
Gray	90	5	—	—	—	5	—
Humpback	—	55	—	—	15	—	30
Minke	—	65	—	—	30	—	5
Northern right	—	100	—	—	—	—	—
Southern right	—	100	—	—	—	—	—
Sei	—	80	5	—	5	5	5
Sperm	5	—	10	60	5	5	15

*Fishes found at depths of around 200 to 1,000 m (660 to 3,300 ft; see Fig. 16.1).

Table 9.2 Status and Estimated Numbers of Great Whales

Whale Species	Status*	Estimated Pre-exploitation Number	Estimated Number in the Late 1990s/Early 2000s
Blue	Endangered	160,000–240,000	5,000
Bowhead	Lower risk	52,000–60,000	7,000–8,000
Bryde's **HUNTED**	Data deficient	100,000	40,000–80,000
Fin	Endangered	300,000	55,000–60,000
Gray (eastern Pacific) **HUNTED**	Lower risk	15,000–20,000	22,000–26,000
Gray (western Pacific)	Lower risk	1,500–10,000	100–200
Gray (Atlantic)	Extinct	Unknown	0
Humpback	Vulnerable	150,000	20,000
Minke **HUNTED**	Lower risk/near threatened	130,000–250,000	850,000
Northern right **HUNTED**	Endangered	Unknown	870–1,000
Southern right	Lower risk	100,000	1,500–4,000
Sei	Endangered	100,000	55,000
Sperm **HUNTED**	Vulnerable	>2,000,000	400,000–500,000

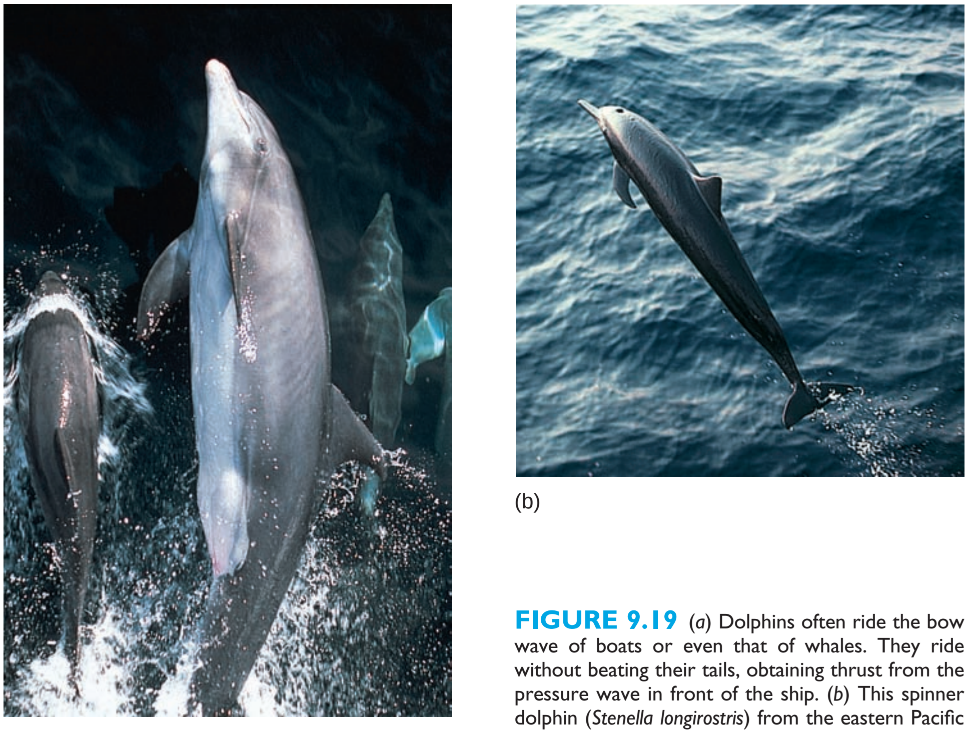
*Status according to CITES (Convention on International Trade in Endangered Species of Wild Flora and Fauna): *endangered*—very high risk of extinction in the near future; *vulnerable*—very high risk of extinction in the medium-term future; *lower risk/near threatened*—not endangered or vulnerable but close to qualifying as vulnerable; *lower risk*—under conservation program, the cessation of which could qualify it as at least vulnerable; *data deficient*—inadequate information to assess risk of extinction.

The largest toothed whale is the sperm whale (*Physeter catodon*), the blunt-nosed giant of *Moby Dick* fame (Fig. 9.18*s*; also see Fig. 1.19). Together, the sperm and baleen whales are often called the **great whales.** There is growing evidence that sperm whales, though toothed, are more closely related to baleen whales than to other toothed whales. The sperm whale is now the most numerous of the great whales, even though it was the mainstay of the whaling industry for centuries (Table 9.2). The largest on record weighed 38,000 kg (42 tons).

Amphipods Small crustaceans whose bodies are compressed from side to side.

- Chapter 7, p. 135; Figure 7.32

> The toothed whales, which include the dolphins and porpoises, lack baleen and feed mostly on fish and squid.



(a)

(b)

FIGURE 9.19 (*a*) Dolphins often ride the bow wave of boats or even that of whales. They ride without beating their tails, obtaining thrust from the pressure wave in front of the ship. (*b*) This spinner dolphin (*Stenella longirostris*) from the eastern Pacific was photographed swimming alongside a ship.

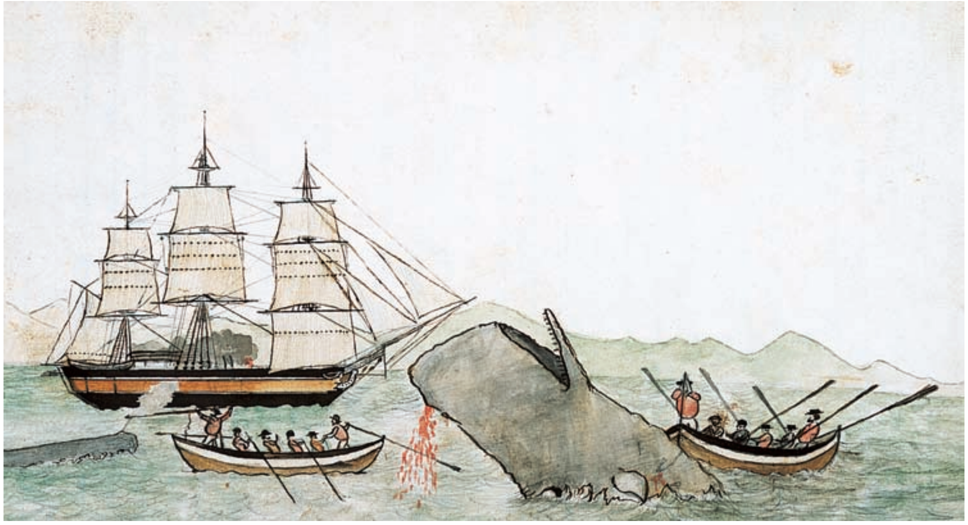


FIGURE 9.20 Sperm whales being harpooned in the South Pacific by the crew of the *Acushnet,* an American whale ship from Fairhaven, Massachusetts. This watercolor painting is part of the sea journal of an 1845 to 1847 voyage. Herman Melville, the author of *Moby Dick,* sailed as a seaman on the *Acushnet* from 1841 to 1842.

Sperm whales are fond of squid, including the giant deep-sea ones. Undigested squid beaks and other debris accumulate in the gut as large globs of sticky material known as **ambergris,** an ingredient in fine perfumes. Sperm whales also eat a wide variety of fishes (including sharks), lobsters, and other marine animals (Table 9.1).

The other toothed whales are much smaller than the great whales. One is the killer whale, or orca (*Orcinus orca;* Fig. 9.18*p*), a magnificent black and white predator with a taste for seals, sea lions, penguins, fishes, sea otters, and even other whales. They use their white bellies to flash and frighten herring schools and their flukes to stun the fish. Killer whales are most common in cold water but are found around the world. Killer whales have a nasty reputation, but there are very few confirmed cases of their attacking humans in the wild.

One of the most enigmatic of whales is the narwhal (*Monodon monoceros;* Fig. 9.18*q*), a small Arctic whale having a long, spiral tusk that can be as long as 2.7 m (9 ft). Narwhal tusks washed ashore apparently gave rise to the legend of the unicorn. The tusk, found only in males, appears to be related to the establishment of a hierarchy of dominance. It has been recently shown, however, that the tusks have a network of small, fluid-filled tubes, which are connected to the narwhal's nervous system, and it has been suggested that they may sense the water for the detection of prey or other chemical cues.

Though they are all whales, most of the small toothed whales are called dolphins or porpoises. Technically, porpoises comprise only a small group of blunt-nosed whales (Fig. 9.18*n*), but in some places the name "porpoise" is given to some of the dolphins.

The many species of dolphins typically possess a distinctive snout, or **beak,** and a perpetual "smile." Playful, highly social, and easily trained, dolphins win people's hearts. They often travel in large groups called **pods,** herds, or schools. They like to catch rides along the bows of boats (Fig. 9.19*a*) or around great whales. The bottlenose dolphin (*Tursiops truncatus*) is the dolphin seen in marine theme parks and oceanaria around the world. The spinner dolphin (*Stenella longirostris;* Figs. 9.18*k* and 9.19*b*) is so named because of its spectacular twisting jumps in the air. It is one of the species of dolphins that get caught in the nets of tuna fishers. This happens because the tuna and dolphins eat the same fish and often occur together.

Whaling Whale hunting, or **whaling,** is an old tradition with a rich history. Stone Age people hunted whales as early as 6000 B.C. Native Americans hunted gray whales in prehistoric times; the aboriginal peoples of the Arctic still legally hunt them. Basques may have hunted them off Newfoundland before Columbus. It was not until the 1600s, however, that Europeans started to substantially exploit the great whales in the North Atlantic. Americans, who eventually dominated worldwide whaling, began hunting off New England in the late 1600s. Whales were harpooned from small, open boats (Fig. 9.20), a technique whalers learned from the natives. It was a rewarding fishery, though not one exploited primarily for food. Blubber provided "train oil," which was used to make soap and used as lamp oil. Baleen was used to make stays for corsets and other goods. Meat and other valuable products also were obtained. Whaling efforts rapidly increased after fast steamships and the devastating explosive harpoon were introduced in the 1800s. The largest and fastest whales, like the blue and fin whales, were then at the mercy of whalers.

Whales are long-lived mammals with a low reproductive rate. The great whales generally give birth to one well-developed calf that has been carried by the mother for a year or more. Females usually don't become pregnant for one or two years after giving birth. As a result of this low reproductive potential, whale stocks could not stand the intense whaling pressure, and many of the fisheries collapsed. Almost all great whales are now classified as endangered (Table 9.2).

The first to be seriously depleted was the slow-swimming North Atlantic right whale (*Eubalaena glacialis;* Fig. 9.18*a*), the "right" species to be killed, according to whalers, because it floated after being harpooned. By the early 1900s whaling had moved to the rich feeding grounds around Antarctica, where other species of whales could be hunted. This location proved to be a bonanza. Whaling nations developed factory ships able to process whole carcasses. The Antarctic fishery reached its peak in the 1930s. The whales received a reprieve during World War II, but it was too late for saving the fisheries. It is estimated that more than a million whales were taken from Antarctica alone.

Blue whales, the largest of them all, were especially sought. A large specimen yielded more than 9,000 gallons of oil. It has been estimated that over 200,000 blue whales were taken worldwide between 1924 and 1971, close to 30,000 during the 1930–1931 whaling season alone. Catches climbed way above the sustainable yield level. Catch per whaler-day's effort declined every year after 1936. As many as 80% of all blue whales caught by 1963 were sexually immature, so that there were even fewer individuals able to perpetuate the species.

Fin whales, the second largest of all whales, became the next major target as blue whales became more and more scarce. The 1950s and early 1960s saw annual catches of 20,000 to 32,000 fin whales per year, mostly from Antarctica. As stocks dwindled, whalers shifted their target again in the mid-1960s, this time to the smaller sei whale (*Balaenoptera borealis;* Fig. 9.18*i*). The sei whale averages a length of around 13 m (44 ft), whereas the fin whale averages 20 m (65 ft).

The abrupt disappearance of the more commercially valuable whales meant lower profits for the whaling industry. In 1946, 20 whaling nations established the **International Whaling Commission (IWC)** in an attempt to regulate whale hunting to stop overfishing. It collected data on the number of whales and set annual quotas for the number of whales to be killed each year, quotas that, unfortunately, were non-binding and could not be enforced. Furthermore, some whaling nations did not belong to the IWC. The blue whale was not completely protected by the IWC until the 1965–1966 season, long after its numbers had been drastically reduced; by then blue whales were so hard to find that the fishery for them was no longer profitable. Even under the protection of the IWC, blue whales were hunted at least until 1971 by countries that did not belong to the IWC.

Intense whaling has led to the near extermination of most species of great whales. Practically all these species are now endangered.

Under mounting pressure from conservationists, the IWC gradually banned the hunting of other whales. Demand for whale products, mostly oil used in the manufacture of margarine and lubricants, was reduced because substitutes had been found for most of them. Whale meat, however, continued to be used as pet food and is still valued as human food, mostly in Japan. The lower quotas of the IWC were, unfortunately, not always accepted by all nations.

The United States Congress passed the **Marine Mammal Protection Act of 1972,** which bans the hunting of all marine mammals in U.S. waters (except in the traditional fisheries of Alaskan natives; see Fig. 4.2) and the importation of marine mammal products. By 1974 the IWC had protected the blue, gray, humpback, and right whales around the world, but only after their stocks were no longer economically viable. Sperm, minke, fin, and sei whales were still hunted in large numbers, but worldwide catches began to dwindle. Catches of these whales fell from 64,418 in 1965 to 38,892 in 1975 and to 6,623 in 1985. A moratorium on all commercial whaling was declared by the IWC in 1985, a move long sought by conservation groups. The former Soviet Union halted all whaling in 1987. Japan, Iceland, and Norway, however, opted in 1988 to continue hunting minke, fin, and sei whales, as allowed by the IWC under the controversial title of "scientific whaling."

In 1994 the IWC created a vast sanctuary for all whales in the waters around Antarctica, the main feeding ground for 80% of the surviving great whales. Japan, however, decided to continue scientific hunting of whales in Antarctica. Starting with the 1997–1998 season, Japan took 440 minkes from Antarctica and 100 from the North Pacific each season until 2002, when it expanded its North Pacific catch to include 150 minke, 50 Bryde's (*Balaenoptera edeni;* Fig. 9.18*d*), 10 sperm, and, for the first time since 1987, 50 sei whales. Japan's quota for 2006 was 1,013 minkes, 50 Bryde's, 10 sperm, 100 sei, and 10 fin whales.

In 2006 the 70-nation IWC abandoned the conservationist policies of its 2003 Berlin Initiative on the belief that the stocks of many of the whale species were large enough to support sustainable whaling. Norway had already resumed commercial whaling in 2005 by setting itself an annual quota of 796 North Sea minkes (Fig. 9.21). Iceland, which had not hunted whales commercially since 1989, then joined Norway in 2006 to further break the 1985 ban on commercial whaling when it started hunting 9 fins and 30 minkes (plus around 40 for scientific purposes) a year. The resumption of commercial whaling by other nations is not far off.

Small-scale whaling remains part of the traditional fisheries of the native inhabitants of the Arctic region from Greenland to Siberia and in the Lesser Antilles in the Caribbean. One of the whales hunted in the Arctic, the bowhead, and another in the Lesser Antilles, the humpback, are endangered. Other smaller whales—the killer whale, narwhal, and beluga (*Delphinapterus leucas;* see Figs. 9.18*o* and 9.27)—are also hunted in the Arctic.

Nobody knows when the great whales will again roam the oceans in numbers approaching those before the start of large-scale whaling. Some experts are afraid that a few critically endangered species will never recover completely. Recovery is nevertheless under way in some species. The California gray whale, protected since 1947, has made a phenomenal comeback (Fig. 9.22). It was removed from the endangered species list in 1994. In 1997 the IWC allowed the killing of 600 gray whales by native hunters in Siberia and 20 gray whales by the Makah Indian tribe in Washington State. The tribe has, however, only taken a single whale, in 1999. Resumption of the hunt has been stopped awaiting the result of court litigation. Even the blue whale, whose reproduction is severely limited by its restriction to small populations scattered around the world, is making a comeback of sorts. It has returned to the Arctic Ocean north of Norway, a region where they flourished before their near extermination by whalers. Sightings off California have increased sharply. Their numbers in Antarctica, however, are even lower than first estimates: around 500 animals, or only 0.2% of those feeding there before whaling began.

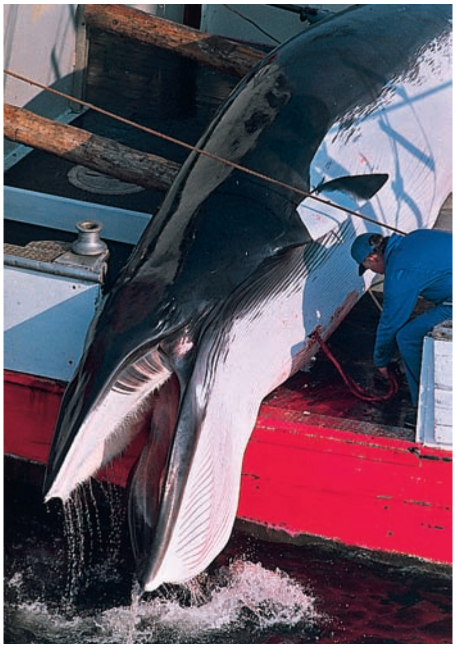


FIGURE 9.21 A harpooned minke whale (*Balaenoptera acutorostrata*) being hauled on board a Norwegian whaling ship in the North Sea.

Dolphins are also at great risk (see Table 18.1, p. 416). They have replaced the larger whales as the most threatened of all cetaceans. As many as 28 species of small cetaceans are in immediate danger of extinction. Less than 600 *vaquitas,* or "little cows" (*Phocoena sinus;* Fig. 9.18*m*), are left. This shy, shovel-nosed porpoise, known only from the northern Gulf of California, remained unknown to science until 1958. Everywhere, fishers are depleting stocks of fish and squid on which dolphins feed. Dolphins themselves are being hunted for human food. The rarest of all dolphins is the Yangtze River dolphin, or *baiji* (*Lipotes vexillifer*), a freshwater dolphin found only in that Chinese river. It is possibly extint by now.

FIGURE 9.22 California gray whales (*Eschrichtius robustus*) are once again a common sight along their long migration routes from Alaska to Mexico (see Fig. 9.32). This species was removed from the endangered species list in 1994.

Tuna fishers using giant purse seine nets (see Fig. 17.6*b*) sometimes trap and drown the many dolphins that often swim above schools of tuna, mostly yellowfin tuna (*Thunnus albacares*) in the eastern Pacific. During the early 1970s an estimated 200,000 dolphins died annually, mostly at the hands of American fishing fleets. The slaughter induced such public outrage that the United States, through the Marine Mammal Protection Act of 1972, called for a reduction in the accidental deaths of dolphins. It imposed a quota of 20,500 for the number of dolphins that could be killed by American fleets. The use of special nets was enforced, and observers were placed on board vessels to verify compliance with the ruling. By 1990 it was estimated that the number of dolphins killed by the United States tuna fleet, by then operating in western Pacific waters, had reached zero. Environmentalists won a major victory when in 1990 the three biggest tuna packers in the United States pledged not to buy or sell fish that was caught using methods that injure or kill dolphins. Tuna cans began to display "dolphin-safe" labels, and imported tuna caught without the use of dolphin-safe methods were banned from sale in the United States. In 1997 the ban was lifted from some countries, notably Mexico, where fishers improved their methods.

Dolphins have also been entangled and killed by the thousands in **drift nets** (see Fig. 17.6*a*), which also threaten sharks, sea turtles, seals, seabirds, and other marine life (Fig. 9.23). The nets, some as large as 60 km (37 mi) long and 15 m (50 ft) deep, have been used to catch fish and squid, but they actually catch practically anything that tries to swim by. Not only do they deplete valuable commercial fisheries like albacore tuna and salmon, but they also trap many noncommercial species. Drift nets are very wasteful because a large percentage of the catch drops out during hauling. Their use in the North Pacific salmon fishery has been particularly deadly to the Dall porpoise (*Phocoenoides dalli;* Fig. 9.18*l*). Hundreds of fishing boats outfitted for drift netting have been used to catch tuna in the South Pacific with potentially disastrous results. International pressure persuaded Japan, which had the largest fleet of drift-net boats in the Pacific, and Taiwan to end the use of drift-net fishing in 1993.

Biology of Marine Mammals

It is surprising how little we know about marine mammals. Most are difficult or impossible to keep in captivity or even to observe for long periods at sea. Some whales and dolphins are rarely seen, so what little we know about them comes from captive or stranded individuals and information gathered over the years by whalers.

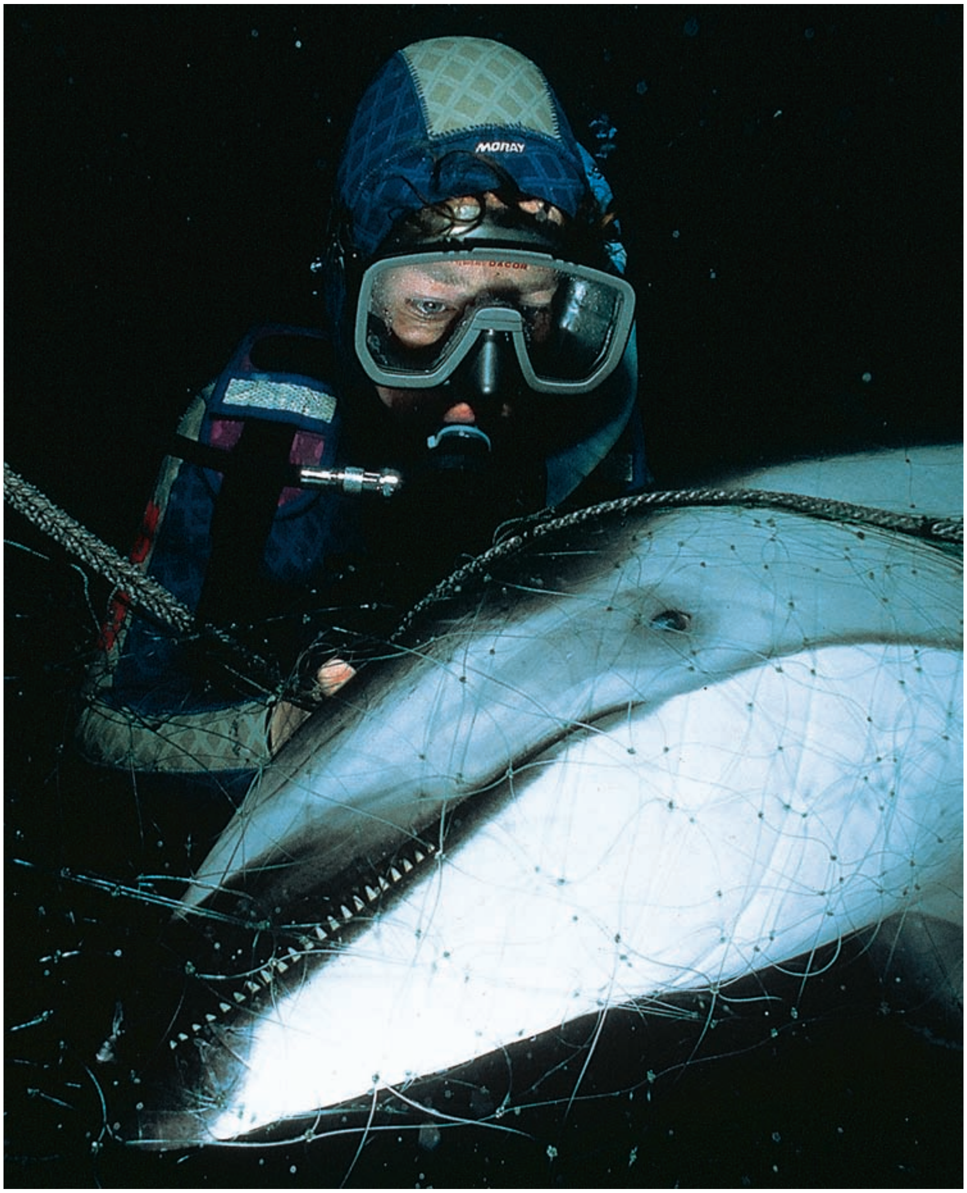


FIGURE 9.23 This Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) drowned after getting caught in a drift net in the North Pacific.

Swimming Streamlining of the body for swimming is a hallmark of marine mammals. Seals, sea lions, and other pinnipeds swim mostly by moving their flippers. Sirenians and cetaceans, in contrast, move their tails and flukes up and down (Fig. 9.24), whereas fishes move their tails from side to side (see Fig. 8.11). Sea lions have been timed at speeds of 35 kph (22 mph), blue and killer whales at 50 kph (30 mph). A group of common dolphins (*Delphinus delphis;* Fig. 9.18*j*) was recorded bowriding at a speed of 64 kph (40 mph).

Cetaceans have the advantage of having the blowhole on top of the head. This allows them to breathe even though most of the body is under water, although many pinnipeds and dolphins jump clear out of the water to take a breath when they are swimming fast (see Fig. 1.4). It also means that cetaceans can eat and swallow without drowning. To avoid inhaling water, marine mammals take very quick breaths. A fin whale can empty and refill its lungs in less than two seconds, half the time we take, even though the whale breathes in 3,000 times more air!

In the large whales, the moisture in their warm breath condenses when it hits the air. Together with a little mucus and seawater, this water vapor forms the characteristic **spout,** or **blow** (Fig. 9.25). The spout can be seen at great distances, and its height and angle can be used to identify the whale (Fig. 9.25). The blue whale, for instance, has a spout some 6 to 12 m (20 to 40 ft) high.

To keep warm in cold water, the great whales depend on a thick layer of blubber (see Fig. 4.2). Feeding, however, leaves their huge mouths exposed to low temperatures, a major problem in the very cold polar waters where they normally feed. A network of blood vessels in their tongues reduces heat loss by transferring heat from warm blood into vessels that carry it back to the body core.

Diving Marine mammals have mastered the art of diving, and most make prolonged dives to considerable depths for food. There is a wide range in diving ability. Sea otters can dive for only 4 or 5 minutes, to depths of perhaps 55 m (180 ft).

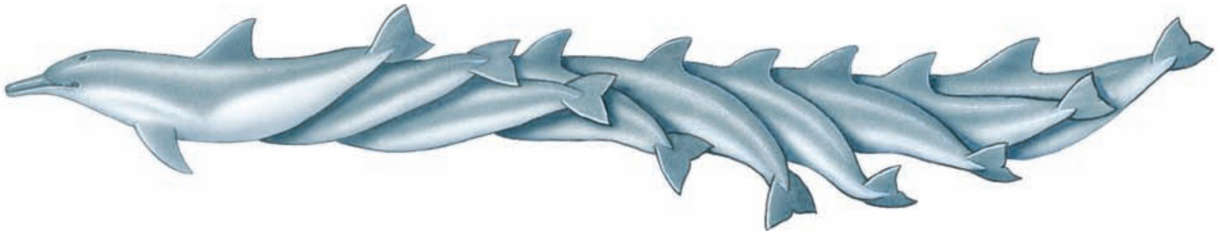


FIGURE 9.24 Cetaceans swim with strong up-and-down movements of the tail and flukes.

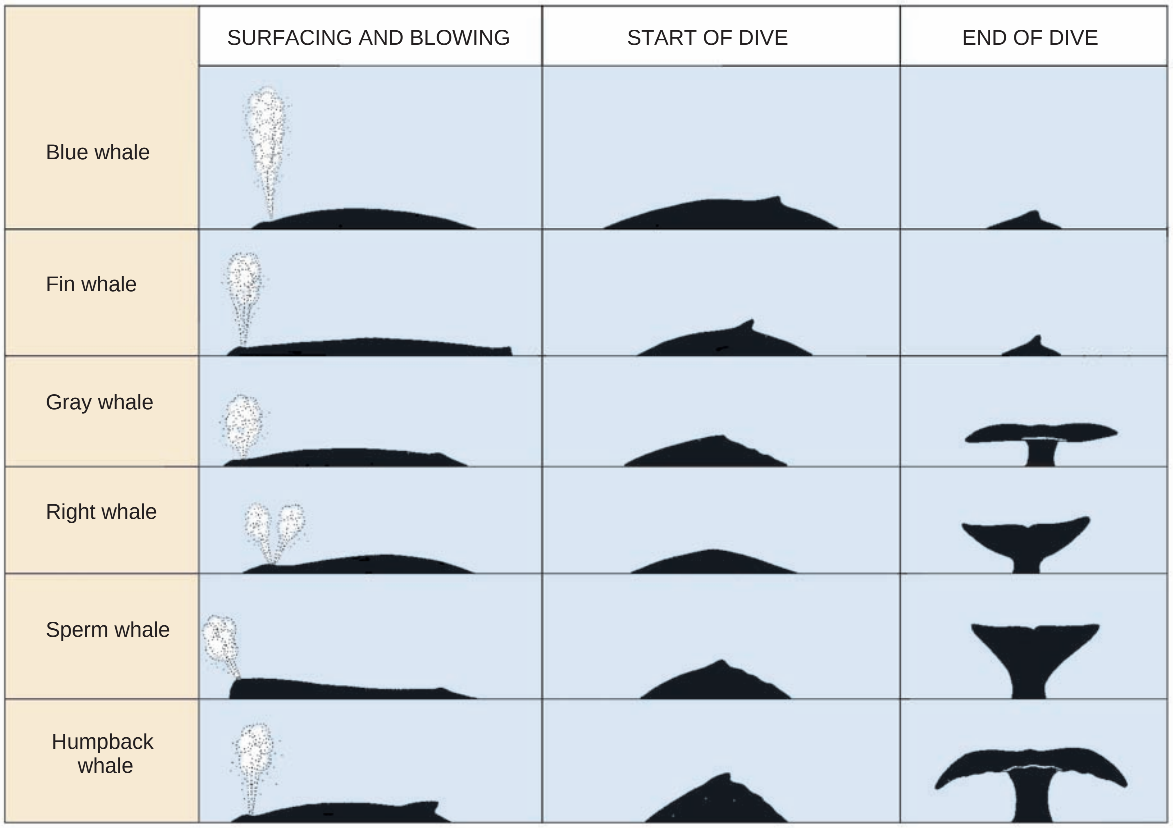


FIGURE 9.25 Great whales can be identified from a distance by their blowing pattern, their outline on the surface, and the way they dive.

Pinnipeds normally dive for up to 30 minutes at maximum depths of 150 to 250 m (490 to 820 ft). Female northern elephant seals (*Mirounga angustirostris*), however, are capable of continuous deep dives of up to 400 m (1,300 ft). One individual was recorded diving to a depth of 1,500 m (5,000 ft). The Weddell seal (*Leptonychotes weddelli*) has been recorded diving for as long as 1 hour 13 minutes and as deep as 575 m (1,900 ft).

The plankton-feeding habits of baleen whales do not require them to dive too deeply for their food, and they seldom venture below 100 m (300 ft). Toothed whales, however, are excellent divers. Dolphins are known to dive as deep as 300 m (990 ft). Though sperm whales are known to dive to 2,250 m (7,380 ft) for at least an hour, beaked whales are the champion divers. The Cuvier's beaked whale (*Ziphius cavirostris;* Fig. 9.18*t*) regularly dives to more than 1,000 m (3,300 ft) to catch the deep-water squids that make up most of its diet. The deepest recorded dive of a beaked whale was close to 1,900 m (about 6,230 ft) for up to 85 minutes.

The long, deep dives of marine mammals require several crucial adaptations. For one thing, they must be able to go a long time without breathing. This involves more than just holding their breath, for they must keep their vital organs supplied with oxygen. Being homeotherms means that marine mammals must use energy to keep their temperature constant—and the release of energy by **aerobic respiration** requires oxygen. To get as much oxygen as possible before dives, most marine mammals and some seabirds take several deep breaths, then rapidly exhale, a behavior known as **apneustic breathing** (Fig. 9.26). As much as 90% of the oxygen contained in the lungs is exchanged during each breath, in contrast to 20% in humans. Many marine mammals have elastic tissues in their lungs and diaphragms, which helps lungs fill and empty rapidly and efficiently.

Marine mammals are also better than other mammals at absorbing the oxygen from the air and storing it in their blood. To start with, they have relatively more blood than non-diving mammals. Their blood also contains a higher concentration of erythrocytes, or red blood cells, and these cells carry more **hemoglobin.** Furthermore, their muscles are extra-rich in **myoglobin,** which means that the muscles themselves can store a lot of oxygen.

Marine mammals have adaptations that reduce oxygen consumption in addition to increasing supply. When they dive, the heart rate slows dramatically, an automatic reflex known as **bradychardia.** Diving bradychardia has been recorded in many diving vertebrates, including humans. It is thought to have evolved as an oxygen-conserving mechanism. In the northern elephant seal, for example, the heart rate decreases from about 85 beats per minute to about 12. Blood flow to non-essential parts of the body, like the extremities and the intestine, is reduced, but it is maintained to vital organs like the brain and heart. Thus, oxygen is made available where it is needed most when oxygen supply is cut off during a dive.

The reduction or absence of oxygen triggers the muscle cells of many animals (including humans during exercise) to carry out

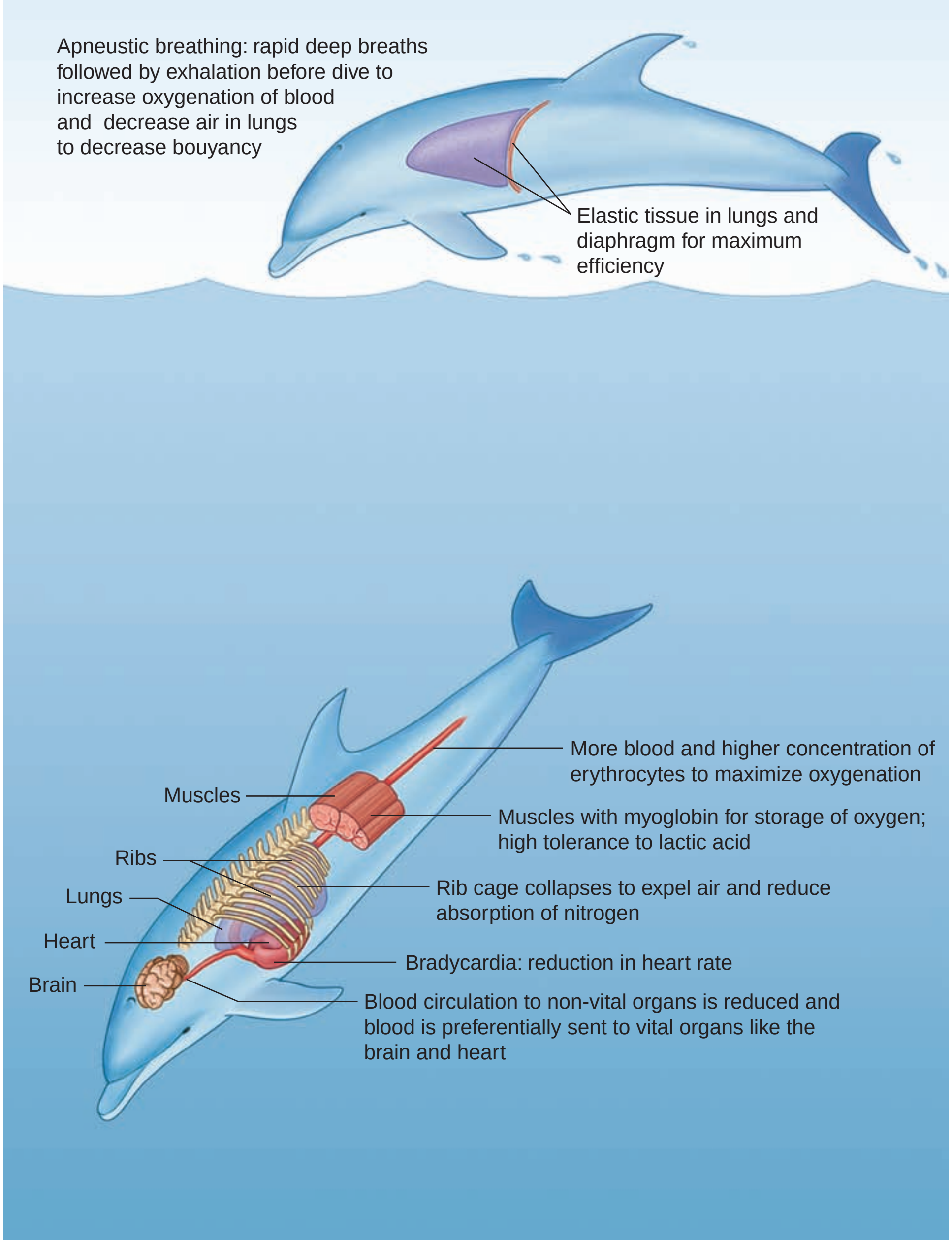

Apneustic breathing: rapid deep breaths followed by exhalation before dive to increase oxygenation of blood and decrease air in lungs to decrease bouyancy
Elastic tissue in lungs and diaphragm for maximum efficiency
Muscles
Ribs
Lungs
Heart
Brain
More blood and higher concentration of erythrocytes to maximize oxygenation
Muscles with myoglobin for storage of oxygen; high tolerance to lactic acid
Rib cage collapses to expel air and reduce absorption of nitrogen
Bradycardia: reduction in heart rate
Blood circulation to non-vital organs is reduced and blood is preferentially sent to vital organs like the brain and heart

FIGURE 9.26 Marine mammals have evolved a series of adaptations that allow them to undertake long, deep dives.

anaerobic respiration, an "emergency" **aerobic respiration** that releases, though inefficiently, some energy without the need of oxygen. A product of anaerobic respiration is **lactic acid,** a chemical that produces cramps and is detrimental to muscular function. The tissues of marine mammals, however, have evolved a high tolerance to the accumulation of lactic acid, another adaptation to increase diving efficiency.

Another potential problem faced by air-breathing, diving animals (including human divers) results from the presence of large amounts of nitrogen (70% of total volume) in the air. Nitrogen dissolves much better at high pressures, like those experienced at depth. The blood of scuba divers picks up nitrogen while they are below the surface. If the pressure is suddenly released, some of the nitrogen will not stay dissolved and forms tiny bubbles in the bloodstream. You can see a similar phenomenon when you open a bottle of soda pop. As long as the top is on, the contents are under pressure. The carbonation, actually carbon dioxide gas (CO_2), remains dissolved. When you open the bottle, the pressure is released and bubbles form. When nitrogen bubbles form in the blood after diving, they can lodge in the joints or block the flow of blood to the brain and other organs. This produces a painful condition known as the **bends,** or decompression sickness. To avoid the bends, human divers must be very careful about how deep they go, how long they stay under water, and how fast they come up.

Marine mammals dive deeper and stay down longer than human divers, so do they get the bends? Marine mammals do have adaptations that prevent nitrogen from dissolving in the blood. Human lungs work pretty much the same while scuba diving under water as on land. When marine mammals dive, on the other hand, their lungs actually collapse. They have a flexible rib cage that gets pushed in by the pressure of the water. This, and increased water pressure with the increased depth, squeezes the air out of peripheral areas of the lungs where it readily dissolves into the blood. Air is moved instead into the central spaces of the lungs, where little nitrogen is absorbed. High concentrations of hemoglobin and myoglobin store the oxygen that marine mammals need in the blood and muscles during dives. Less air is thus needed in the lungs, which reduces the amount of nitrogen that can be absorbed. Apneustic breathing, exhaling before a dive, further reduces the amount of air—and therefore nitrogen—in the lungs. A reduction in the amount of

Aerobic Respiration

organic matter + O_2 $\xrightarrow{\text{in all cells}}$ CO_2 + H_2O + energy
(glucose)

- Chapter 4, p. 67

Hemoglobin A blood protein that transports oxygen in many animals; in vertebrates it is contained in *erythrocytes,* or red blood cells.
Myoglobin A muscle protein in many animals that stores oxygen.

- Chapter 8, p. 164

Anaerobic Respiration

organic matter $\xrightarrow{\text{in muscles}}$ energy + lactic acid
(glucose)

- Chapter 4, p. 68

EYE ON SCIENCE

The Bends in Cetaceans

Cetaceans and other marine mammals, many of which are deep divers, have been thought of as being adapted to reduce the amount of nitrogen that dissolves in their blood during deep dives, thus preventing the bends (see "Diving," p. 197). Scientists have gathered evidence that this may not be true after all, at least in sperm whales, the deepest diver among cetaceans.

Scientists from the Woods Hole Oceanographic Institution in Massachusetts in the United States studied the skeletons of Atlantic and Pacific sperm whales collected more than 100 years ago. The skeletons showed the same characteristic damage and loss of bone tissue that has been described in the skeletons of humans who have suffered from the bends. Bones in the ribs and other parts of the body showed clear degeneration and erosion, which covered them with tiny holes. The formation of bubbles of nitrogen in the thin blood vessels that permeate bone caused the blood vessels to burst, thus inducing the eventual degeneration and erosion of the bone tissue. Similar changes were also observed in cartilage. There was no evidence that microbial infections were responsible for the lesions, and the severity of the lesions was observed to increase with the size, and thus the age, of the whales.

Researchers concluded that the bone and cartilage lesions were caused by the cumulative effect of changes in normal diving behavior, as when whales are forced to surface faster than normal. Injuries to internal tissue have also been described in other species of whales that, when feeding in deep water, surface far too fast panicked by powerful military sonars. These injuries appear to have also been caused by the formation of nitrogen bubbles, another piece of evidence that whales are not completely resistant to the bends.

Some investigators, however, have questioned the link between long-term deep diving and cetacean bone lesions. One researcher has even suggested that the lesions in the preserved bones may reflect the impact of mechanized whaling. In the meantime, there has been additional evidence on the effect of nitrogen formation on the mass stranding of small whales, including pilot whales and dolphins. Three species of beaked whales also showed similar lesions following a mass stranding after exposure to sonar signals.

The Woods Hole team is studying additional sperm whale specimens and the skeletons and tissues of stranded whales, especially when the tissues are fresh. They also plan to survey other marine mammals in search of the lesions found in sperm whales. They also hope to investigate the diving behavior of whales and seals to see if certain types of behaviors help avoid the bends. What behaviors might be involved? What other types of adaptations may have evolved in the circulatory and respiratory systems of deep-diving marine mammals to help them avoid the bends?

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

air in the lungs has the additional advantage of decreasing buoyancy, which makes descents to deep water easier.

The long-held view that marine mammals don't get the bends may not be accurate after all. Evidence shows that deep-diving whales suffer from some of the effects of the bends (see "The Bends in Cetaceans," above).

Adaptations for deep, prolonged dives in marine mammals include the efficient exchange of air on the surface, the storage of more oxygen in the blood and muscles, a reduction of the blood supply to the extremities, and collapsible lungs to help prevent the bends.

Echolocation Marine mammals depend little on the sense of smell, which is so important to their terrestrial cousins. Their vision is excellent, but they have developed **echolocation,** another sensory system based on hearing. Echolocation is nature's version of sonar. Most if not all toothed whales, including dolphins and porpoises, and some pinnipeds are known to echolocate. At least some baleen whales may also use echolocation. Echolocation is not exclusive to marine mammals. Bats, for example, use it to find insects and other prey while flying at night.

Marine mammals echolocate by emitting sound waves, which travel about five times faster in water than in air, and listening for the echoes reflected back from surrounding objects (Fig. 9.27). The brain then analyzes the echoes. The time it takes the echoes to return tells the animals how far away the object is.

Many marine mammals echolocate by analyzing the echo of sound waves they emit. Echolocation is used to find prey and orient to the surroundings.

The sounds used in echolocation consist of short bursts of sharp clicks that are repeated at different frequencies. Low-frequency clicks have a high penetrating power and can travel long distances. They reflect from large features and are used to obtain information on the surrounding topography. Low-frequency sound waves may also be used in some toothed whales to stun their prey (see "The Other 'Big Bang Theory'," p. 201). To discriminate more detail and locate nearby prey, high-frequency clicks that are inaudible to humans are used. Experiments have shown that blindfolded bottlenose dolphins can discriminate between objects of slightly different size or made of different types of materials and can even detect wires.

We are not completely sure how echolocation operates in marine mammals. Cetaceans produce clicks, squeaks, and whistles as air is forced through the air passages and several associated air sacs while the blowhole is closed (Fig. 9.27). The frequency of the clicks is changed, or modulated, by contracting and relaxing muscles along the air passages and sacs. A fatty structure on the forehead of toothed whales, the **melon,** appears to focus and direct the outgoing sound waves.

The melon gives these whales their characteristic rounded foreheads. To accommodate the melon, the skull is modified

The Other "Big Bang Theory"

Toothed whales use sound for echolocation and for communication with each other. Recently, a different use of sound waves by these cetaceans has been suggested.

This hypothesis developed as a possible explanation for the feeding habits of sperm whales, the largest of the toothed whales. Squids taken from the stomach of captured and stranded whales often show no tooth marks or scars of any kind. In fact, live squids have been known to swim out of the stomachs of freshly caught whales! It seems that sperm whales have a way of catching squids—including giant squids—without using their teeth, even if their teeth are actually of little help because they are present only in the lower jaw. Another puzzle is explaining how sperm whales weighing 36,000 kg (40 tons) or more and averaging speeds of just 2 to 4 knots catch squids that can swim at 30 knots.

How about the possibility that whales and dolphins use powerful blasts of sound to catch their food? This ingenious hypothesis has been dubbed a second "big bang theory," the original being the well-known view proposed to explain the origin of our universe (see "The Structure of the Earth," p. 20). Catching prey whole and still alive can be explained if the whale stuns its prey with a blast of sound and then simply swallows it whole.

Some indirect evidence is provided by the now-extinct ancestors of toothed whales. Fossils of the earliest known toothed whales have long snouts armed with many piercing teeth (see "The Whales That Walked to Sea," p. 192). Like those of a barracuda, the teeth were probably used to catch small fish and other prey. The long snout, however, has disappeared in most modern cetaceans, and the teeth have become wider and shorter. Have modern toothed whales evolved a new technique to catch their food, or has their food source changed?

Sonic hunting may involve a beam of low-frequency sound waves powerful enough to stun a fish or squid. Although the sophisticated sound-producing mechanism of cetaceans is not fully understood, sperm whales do produce the required sound waves, the strongest and loudest of any animal. Sonic hunting may have evolved as a by-product of echolocation in the early toothed whales.

It is not easy to obtain the necessary evidence to support this hypothesis. Loud noises can indeed stun fish, but it is difficult to reproduce the exact sounds produced by cetaceans. Dolphins living in the wild have produced gun-like bangs that can be heard by humans. Unfortunately, undertaking detailed studies of sonic hunting in the wild presents many complications. Captive dolphins do not produce loud noises, which is not surprising because the echo of the noise off the tank walls would be very painful to them. The function of big bangs in whales is but one of the many surprising adaptations of cetaceans waiting to be explored.

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to form a pointed, dish-shaped face. The skull is also asymmetric, the right side being slightly different from the left side. Belugas (Fig. 9.28) have a bulging forehead, which changes shape as the melon, moved by muscles, focuses the sound. The huge forehead of the sperm whale is filled in part with a massive melon called the **spermaceti organ.** Whalers originally thought this was the sperm sac of the whale, hence the peculiar name. This organ is filled with a waxy oil, **spermaceti,** once much sought after for making candles and still used as a lubricant for precision instruments. The actual function of the spermaceti organ is a controversial issue. It has been suggested that the deep-diving sperm whale might also use the spermaceti organ to regulate buoyancy or to absorb excess nitrogen, keeping it out of the bloodstream.

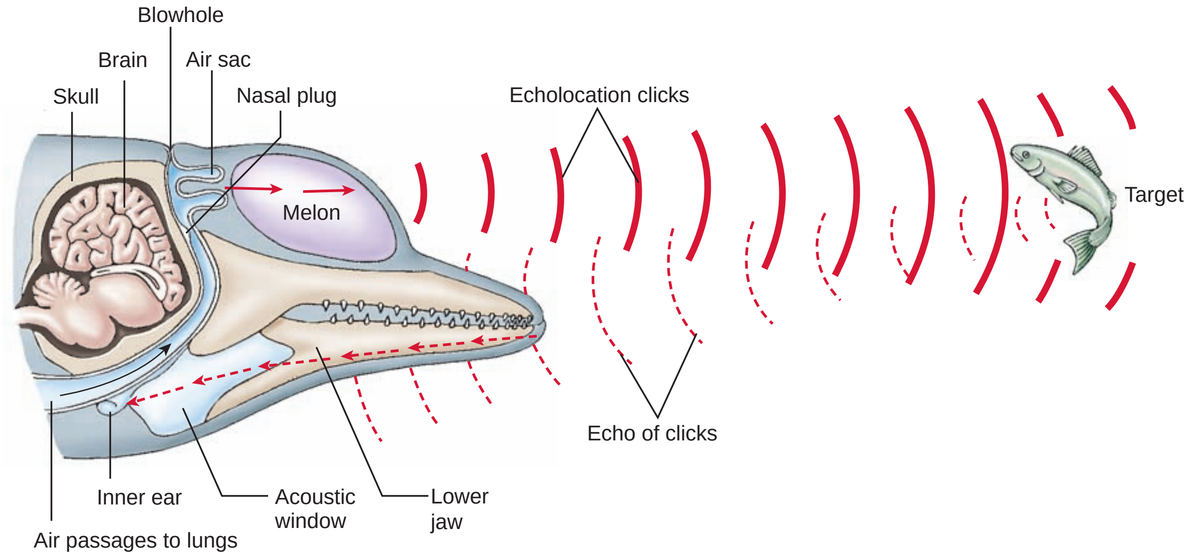
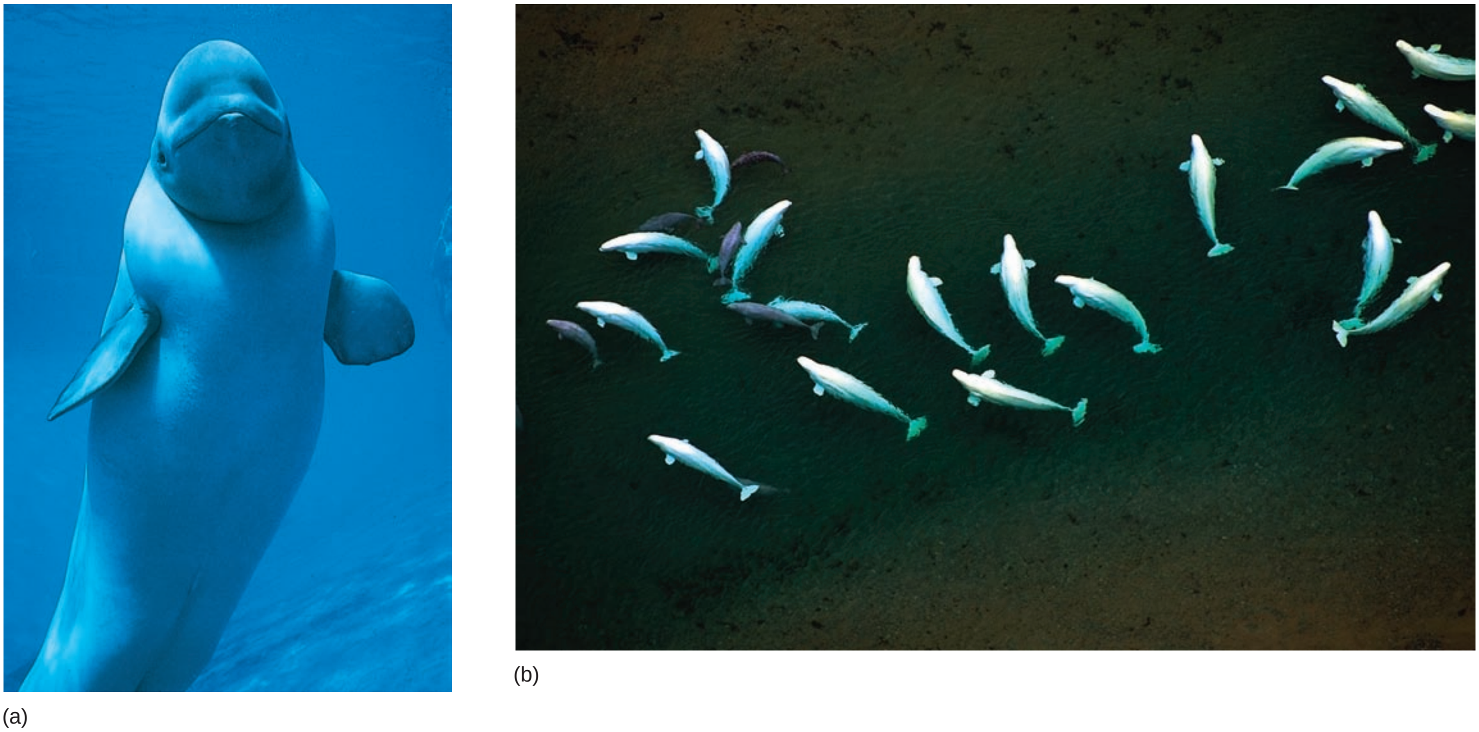


FIGURE 9.27 Dolphins echolocate by emitting bursts of sound waves, or clicks, as air is pushed through internal air passages. Two muscular nasal plugs act as valves, closing and opening the passages. Flaps of tissue on the plugs probably also produce sound by vibrating in the moving air. The clicks are focused into a beam by the melon. To cover a wider area, the dolphin moves its head from side to side. The melon is also known to receive the echoes and transmit them to the ears, but most are received by the lower jaw.


(a)

(b)

FIGURE 9.28 (*a*) The beluga (*Delphinapterus leucas*) is a white Arctic whale (*beluga* means "white one" in Russian) with a conspicuous melon. (*b*) In their natural environment belugas live in small groups.

In toothed whales incoming sound waves are received primarily by the lower jaw (Fig. 9.27). The ear canal that connects the outside with the inner ear is reduced or blocked in most cetaceans. The jawbones, filled with fat or oil, transmit sound to the two, very sensitive inner ears. Each ear receives sound independently. The ears are protected by a bony case and embedded in an oily mixture that insulates the ear but allows sound waves to pass from the jaws. Sound information is sent to the brain, which forms a mental "picture" of the target or surroundings. In fact, sight and sound information seems to be handled similarly by the brain. Captive dolphins can recognize by echolocation objects they have seen and recognize by sight those they have previously echolocated.

Behavior The mammalian brain has evolved as an association center for complex behaviors in which learning, not instinct, dominates. In contrast to fishes, birds, and other vertebrates, mammals rely mostly on past experience, stored and processed by the brain, to respond to changes in the environment (see "How Intelligent *Are* Cetaceans?," p. 203).

Most marine mammals are highly social, living in groups at least part of the time. Many pinnipeds live in huge colonies during the breeding season. Most cetaceans spend their entire lives in highly organized pods of a few (Fig. 9.28*b*) to thousands of individuals. Some pods include smaller subgroups organized by age and sex. To keep in contact, many of their highly complex and sophisticated behaviors are directed toward members of their own species.

Sounds, or **vocalizations,** play a prominent role in communication. Sea lions and fur seals communicate by loud barks and whimpers; seals use more sedate grunts, whistles, and chirps. The vocalizations of pinnipeds are especially important in maintaining territories during reproduction (see "Reproduction," p. 206). Females and their pups or calves recognize each other partly by their sounds, partly by smell.

Cetaceans produce a rich variety of vocalizations that are different from the sounds used for echolocation. Both types of sounds can be produced simultaneously, providing further evidence of the complexity of sound production in marine mammals. Social vocalizations are low-frequency sounds that humans can hear. The variety of sounds is amazing and includes grunts, barks, squeaks, chirps, and even "moos." Different sounds are associated with various moods and are used in social and sexual signaling. Whistles, emitted in many variations and tones, are characteristic of each species. Some of these sounds serve as a "signature," allowing individuals of the same species to recognize one another. Male fin whales use high-intensity songs to attract females. Among the more than 70 calls that have been identified among killer whales, some are present in all individuals, whereas others are "dialects" that identify certain pods.

Sounds are also used to maintain the distance between individuals and have an important role in the structure of the pod. Particular sounds are emitted during breeding, feeding, alarms, and birth. Mother gray whales grunt to stay in contact with their calves. Fin whales make a low-pitched sound thought to be involved in long-distance communication. Right whales have at least six distinct calls, each related to a specific function.

The humpback whale is renowned for its soulful songs. They are sung by breeding males to attract females by advertising

How Intelligent *Are* Cetaceans?

We often hear that whales, dolphins, and porpoises are as intelligent as humans, maybe even more so. Are they really that smart? There is no question that cetaceans are among the most intelligent of animals. Dolphins, killer whales, and pilot whales in captivity quickly learn tricks. Bottlenose dolphins have been used to detect underwater mines in murky water.

This type of learning, however, is called **conditioning.** The animal simply learns that when it performs a particular behavior it gets a reward, usually a fish. Many animals, including rats, birds, and even invertebrates, can be conditioned to perform tricks. We certainly don't think of these animals as our mental rivals.

Unlike most other animals, however, dolphins quickly learn by observation and may spontaneously imitate human activities. One tame dolphin watched a diver cleaning an underwater viewing window, seized a feather in its beak, and began imitating the diver—complete with sound effects! Dolphins have also been seen imitating seals, turtles, and even water-skiers.

Given the seeming intelligence of cetaceans, people are always tempted to compare them with humans and other animals. Studies on discrimination and problem-solving skills in the bottlenose dolphin, for instance, have concluded that its intelligence lies "somewhere between that of a dog and a chimpanzee."

Such comparisons are unfair. It is important to realize that intelligence is a very human concept and that we evaluate it in human terms. After all, not many people would consider themselves stupid because they couldn't locate and identify a fish by its echo. Why should we judge cetaceans by their ability to solve human problems?

Both humans and cetaceans have large brains with an expanded and distinctively folded surface, the **cortex.** The cortex is the dominant association center of the brain, where abilities such as memory and sensory perception are centered. Cetaceans have larger brains than ours, but the ratio of brain to body weight is higher in humans. Again, direct comparisons are misleading. In cetaceans it is mainly the portions of the brain associated with hearing and the processing of sound information that are expanded. The enlarged portions of our brain deal largely with vision and hand-eye coordination. Cetaceans and humans almost certainly perceive the world in very different ways. Their world is largely one of sounds, ours one of sights.

Contrary to what is depicted in movies and on television, the notion of "talking" to dolphins is also misleading. Though they produce a rich repertoire of complex sounds, they lack vocal cords and their brains probably process sound differently than ours do. Bottlenose dolphins have been trained to make sounds through the blowhole that sound something like human sounds, but this is a far cry from human speech. By the same token, humans cannot make whale sounds. We will probably never be able to carry on an unaided conversation with cetaceans.

As in chimps, captive bottlenose dolphins have been taught American Sign Language. These dolphins have learned to communicate with trainers who use sign language to ask simple questions. Dolphins answer back by pushing a "yes" or "no" paddle. They have even been known to give spontaneous responses not taught by the trainers. Evidence also indicates that these dolphins can distinguish between commands that differ from each other only by their word order, a truly remarkable achievement. Nevertheless, dolphins do not seem to have a real language like ours. Unlike humans, dolphins probably cannot convey very complex messages.

Bottlenose dolphins (*Tursiops truncatus*) participating in research to test acoustic communication. The devices on their heads, which are held in place by suction cups, light up every time a dolphin whistles.

Observations of cetaceans in the wild have provided some insights into their learning abilities. Several bottlenose dolphins off Western Australia, for instance, have been observed carrying large, cone-shaped sponges over their beaks. They supposedly use the sponges for protection against stingrays and other hazards on the bottom as they search for fish to eat. Only females use sponges as tools, and it appears that this behavior is passed on by mothers to female offspring. This is the first record of tool use and of its cultural transmission in a wild marine mammal.

Instead of "intelligence," some people prefer to speak of "awareness." In any case, cetaceans probably have a very different awareness and perception of their environment than do humans. Maybe one day we will come to understand cetaceans on their terms instead of ours, and perhaps we will discover a mental sophistication rivaling our own.

their readiness to mate. The songs consist of phrases and themes repeated in a regular pattern for a half hour or longer. They may be repeated over and over for days. The songs change over time. Males also start each breeding season with the song they were singing at the end of the previous breeding season. New songs learned from immigrants have been shown to gain instant popularity among native whales. Researchers record and catalog songs to help track whales in their annual migrations.

Communication among cetaceans is not restricted to vocalizations. Researchers have described a variety of postures and movements that may indicate the animal's mood. Dolphins clap their jaws or turn around with their mouths open as a threat. The loud cracking sound made when some marine mammals slap their flukes or flippers on the surface is thought to be a warning signal.

Cetaceans are noted for their **play behavior,** seemingly pleasurable activities with no serious goal. Many species, including the great whales and killer whales, play with food or floating objects like logs, kelp, and feathers, throwing them up in the air or holding and pushing them with their snouts. Individuals may swim head down or on their backs apparently just for the fun of it. Dolphins play with rings of air bubbles they create. Dolphins also like to surf, and pilot (*Globicephala;* Fig. 9.18*r*) and right whales go sailing with their flukes out of the water to catch the wind. Sex play, the

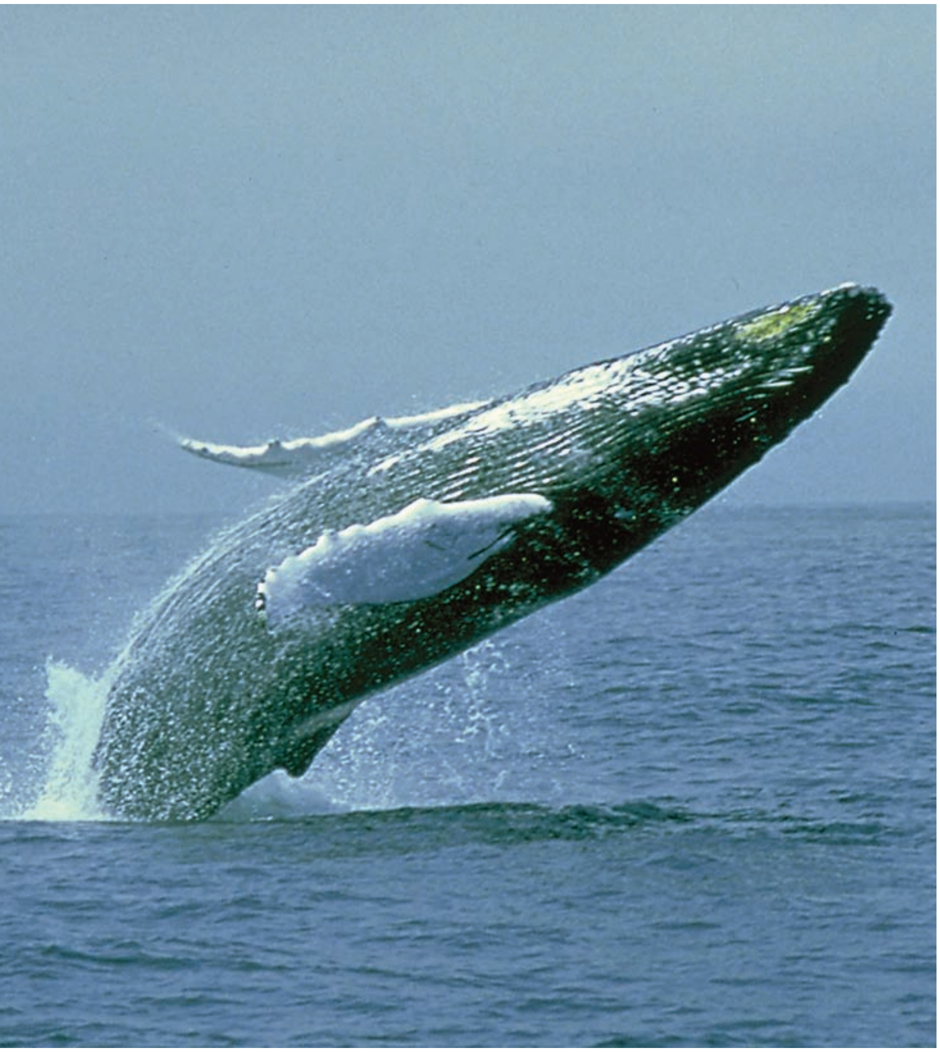


FIGURE 9.29 A humpback whale (*Megaptera novaeangliae*) performing a full spinning breach.

rubbing and touching of the genital opening, is also common.

The sight of a great whale **breaching,** leaping up in the air and loudly crashing on the surface, is awesome (Fig. 9.29). Breaching has been variously interpreted as a warning signal, as a way of scanning the surface or the shoreline, as a means of getting rid of external parasites or an ardent lover, and simply as fun. After a deep dive, sperm whales may breach, fall on their backs, and make a splash that can be heard 4 km (2.5 mi) and seen 28 km (17.4 mi) away! Many whales stick their heads out of the water to spy on their surroundings (Fig. 9.30*b*).

The complex behavior of cetaceans is evident in other ways. When one individual is in trouble, others may come to assist (Fig. 9.30*a*). Members of a pod refuse to leave a wounded or dying comrade. Whalers knew that a harpooned whale was a lure for others, which are drawn from miles around. Dolphins will carry injured individuals to the surface to breathe (Fig. 9.30*c*), and there are records of females carrying the body of a stillborn calf until it rots.

Many toothed whales work together when they hunt, some in coordinated pairs. Sometimes whales take turns feeding while their partners herd a school of fish. An individual may investigate something strange lying ahead while the rest of the group waits for the "report" of the scout. Studies of animals in the wild show that dolphins belong to a complex society, one in which long-term partnerships of members of the same sex play an important role in sexual behavior, parental care, and other aspects of daily life. Social behavior in cetaceans may ultimately show many parallels with social behavior in large-brained mammals such as apes and humans.

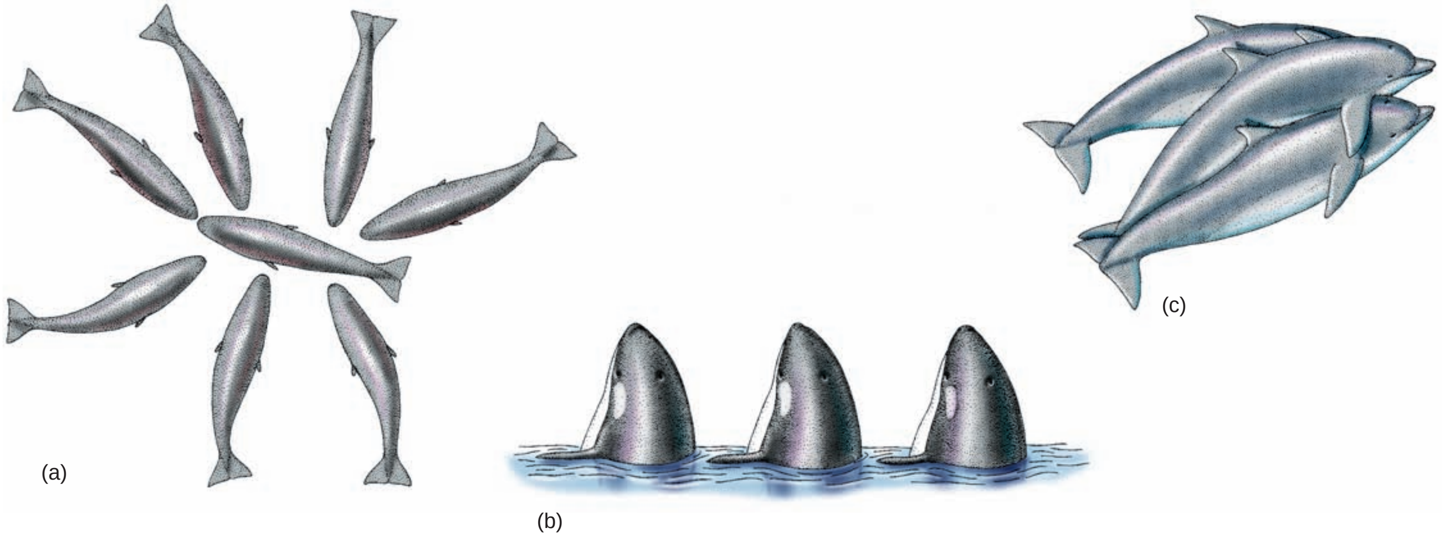


FIGURE 9.30 Whale watchers may be rewarded with examples of the complex behavior of whales: (*a*) sperm whales (*Physeter macrocephalus*) surrounding an injured member of a pod, (*b*) "spying" behavior in killer whales (*Orcinus orca*) in the wild, (*c*) two bottlenose dolphins (*Tursiops truncatus*) carrying a stunned companion to the surface to breathe.

One of the mysteries of the behavior of whales and dolphins is the **stranding,** or **beaching,** of individuals, sometimes dozens, on beaches (Fig. 9.31). The animals refuse to move, and efforts to move them into deeper water usually fail. Even if they are pulled out to sea, they often beach themselves again. The whales die because their internal organs collapse without the support of the water. Stranding has been described in many species, but some, such as pilot and sperm whales, strand themselves more often than others. It appears that whales become stranded when they follow one or more members of their group that have become disoriented by a storm, illness, or injury. This indicates the strong cohesiveness and herd instinct of the group.

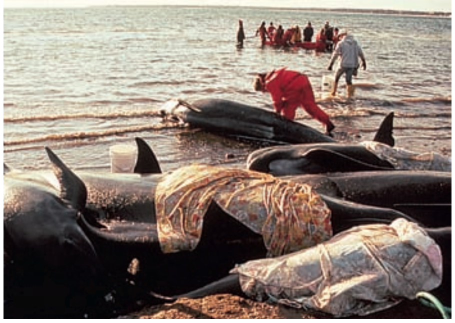


FIGURE 9.31 These pilot whales (*Globicephala melas*) stranded themselves on a beach in Cape Cod, Massachusetts. Only two of the 55 stranded whales survived.

Marine mammals, particularly cetaceans, use a rich variety of vocalizations and tactile and visual signals to communicate with each other. Play behavior and mutual assistance are additional evidence of the complexity of their behavior.

Stranding of whales has recently been linked to high-intensity sonar that uses bursts of intense sound waves. The navies of the United States and other nations have used the sonar to detect enemy submarines. Whales stranding after naval exercises where the sonar was used showed hemorrhages in the brain and inner ears, which cause disorientation and death. Tissue injury may also be caused by the formation of nitrogen bubbles or the bends (see "The Bends in Cetaceans," p. 200). As a result, a 2002 court decision temporarily banned the United States Navy from the worldwide use of the high-intensity sonar. Noise from ship propellers, depth sounders, and sonar used for scientific purposes has also been suggested as disturbing to whales. Dolphins spend more time on the surface and rest less, and killer whale calls last longer, when whale-watching boats are close by.

The relationship between dolphins and humans is a controversial one. Though exaggerations abound, there are authenticated cases of dolphins approaching human swimmers who appeared to be in trouble. For more than a century, fishers in southern Brazil have established a unique partnership with dolphins. The dolphins detect fish and deliver them to fishers waiting with nets. Fishers have learned to interpret cues given by the dolphins about the location and abundance of fish. Generations of dolphins have learned that a row of fishers holding a net in shallow water means an easy catch for themselves, even if it has to be shared with funny-looking, two-legged mammals.

Some people swear of experiencing "spiritual inspiration" while swimming among dolphins during the "dolphin encounters" offered by some resorts. Dolphins trained for military purposes by the former Soviet navy are being used to treat children suffering from behavioral disorders. Other people see this as outright exploitation of the captive animals, and interactions with humans may after all be harmful to dolphins. It has been suggested that stress among captive dolphins reduces their life span.

Migrations Many pinnipeds and cetaceans make seasonal migrations, often traveling thousands of miles from feeding grounds to breeding areas. Male southern elephant seals (*Mirounga leonine*) are known to travel as far as 8,000 km (almost 5,000 mi) to mate. Most toothed whales, on the other hand, do not migrate at all, though they may move about in search of food.

The migrations of the great whales are by far the most remarkable. Many baleen whales congregate to feed during the summer in the productive waters of the polar regions of both hemispheres, where huge concentrations of diatoms and krill thrive in the long days. During the winter they migrate to warmer waters to breed. The seasons are reversed in the Northern and Southern Hemispheres, so, when some humpback whales are wintering in the Hawaiian Islands or the West Indies, other humpbacks living in the Southern Hemisphere are feeding around Antarctica during the southern summer (Fig. 9.32).

Most great whales migrate from winter breeding areas in the tropics to summer feeding areas in colder waters.

The migratory route of the gray whale is the best known of any of the great whales (see Fig. 9.32). From the end of May to late September, the whales feed in shallow water in the northern Bering, Beaufort, and East Siberian seas. They begin moving south in late September when ice begins to form. In November they begin crossing through the eastern Aleutian Islands. They eat less while on the move, burning off close to a quarter of their body weight. The whales cover about 185 km (115 mi) per day. They travel alone or in small groups along the coast of the Gulf of Alaska and down the western coast of North America en route to the Baja California Peninsula in Mexico (see Fig. 9.22). Migrating individuals often show spying behavior, pushing their heads out of the water. This raises the possibility that they navigate by using memorized landmarks. They reach Oregon around late November or early December and San Francisco by mid-December. Females generally migrate earlier. In late February pregnant females are the first to appear in shallow, quiet lagoons in southern Baja California and the southern mainland coast of the Gulf of California. It is here that females give birth and males mate with non-pregnant females.

The northbound migration begins by March, after the birth of the 700 to 1,400 kg (1,500 to 3,000 lb) calves. Females mate every two years, and the first to migrate north are the newly pregnant females that did not give birth. They will return 12 months later to give birth. Mothers with calves leave last. On the way north the whales tend to stay farther from the coast and move slower than on their southward migration, an average of 80 km (50 mi) per day because of the unfavorable currents (see Fig. 3.20) and the newborn calves. The last whales leave the coast off Washington State by early May. They start reaching their feeding areas by late May, completing an amazing eight-month trip of up to 18,000 km (11,200 mi), the longest migration of any mammal.

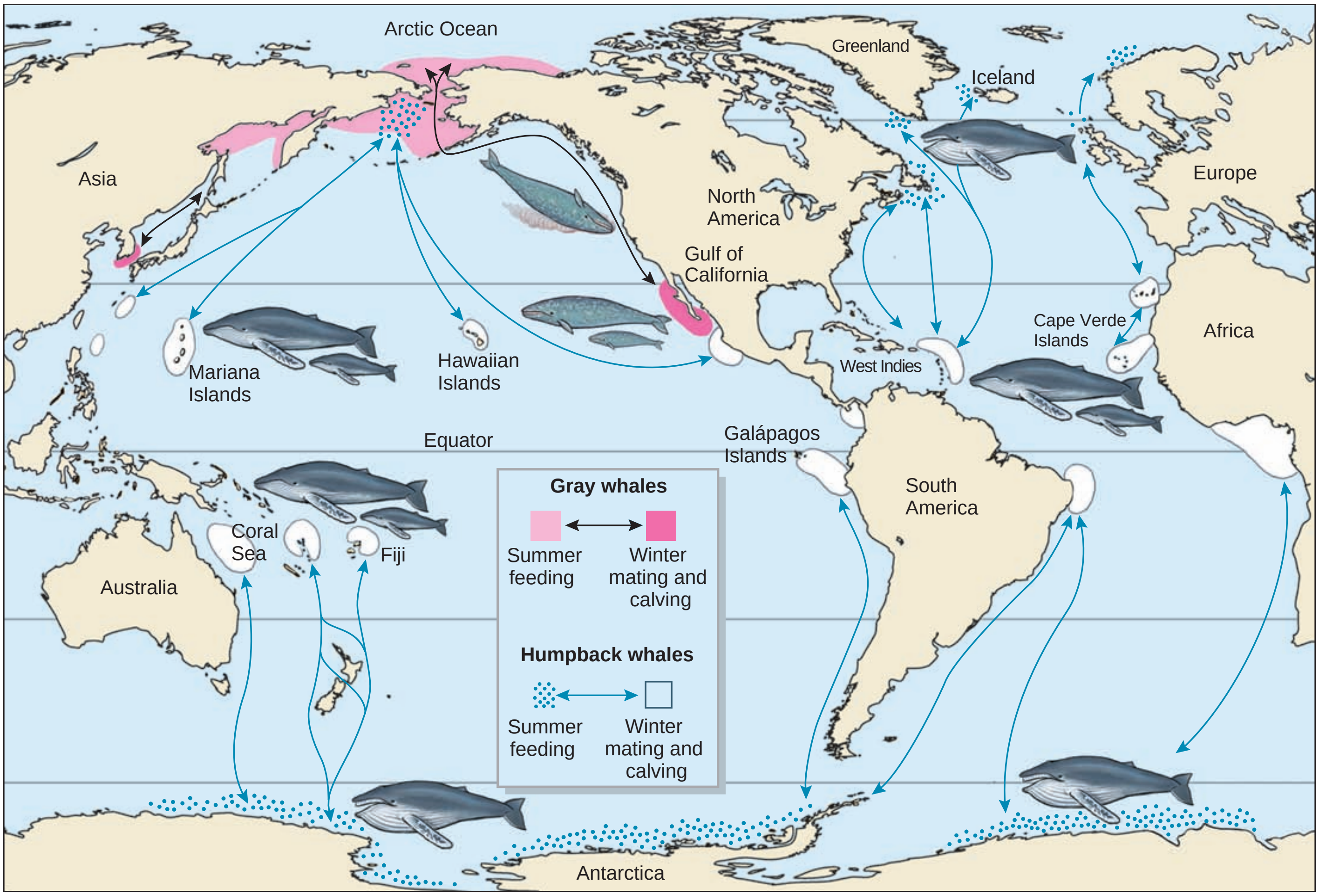

Arctic Ocean
Greenland
Iceland
Asia
Europe
North America
Gulf of California
Cape Verde Islands
Africa
West Indies
Mariana Islands
Hawaiian Islands
Equator
Galápagos Islands
South America
Coral Sea
Fiji
Australia
Antarctica
Gray whales
Summer feeding
Winter mating and calving
Humpback whales
Summer feeding
Winter mating and calving

FIGURE 9.32 Migration routes of humpback (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*). Both species tend to migrate and breed close to shore, where they were easily hunted. Both species are on the comeback, and the gray whale is no longer considered endangered. The western Pacific population of grays that may still breed south of Korea also appears to be making a comeback. Gray whales used to live in the North Atlantic until exterminated in the nineteenth century (also see Fig. 9.22).

There is still much to be learned about the migrations of the gray whale and other whales. One vexing question is how whales navigate. It has been suggested that they use the earth's magnetic field, a possibility that implies that they carry some type of internal compass to orient themselves.

Scientists are using novel ways to investigate the migration of whales. Attaching small radio transmitters to whales and tracking their movements by satellite promises to uncover intriguing details. It has been found, for instance, that some isolated groups of gray whales along the migratory route do not migrate at all. One group resides in the Queen Charlotte Islands off the coast of British Columbia. Gray whales are also known to avoid cities by moving away from the coast. Females and young may slow down their migration back to the Arctic by taking shelter in kelp forests to avoid killer whales. Analysis of the DNA of humpback whale populations in the Hawaiian Islands suggests that, as in the green turtle, individuals always return to the feeding grounds of their mothers.

Reproduction The reproductive system of marine mammals is similar to that of land mammals. They have some unique adaptations to life in the water, however. To keep the body streamlined, male cetaceans and most other marine mammals have an internal penis and testes. The penis, which in blue whales is over 3 m (10 ft) long, is kept rigid by a bone. It is extruded just before copulation through the **genital slit,** an opening anterior to the anus (see Fig. 9.15).

Pinnipeds breed on land or ice, some migrating long distances to isolated islands to do so. In most species of seals each adult male breeds with only one female. Camcorders attached to animals in the wild (see "Eyes (and Ears) in the Ocean," p. 12) have shown that male harbor seals make rumbling noises, quiver their necks, and release a stream of air bubbles, perhaps a display to attract females. In sea lions, fur seals, and elephant seals, however, a male breeds with many females. During the breeding season the males of these species, which are much bigger and heavier than females, come ashore and establish breeding territories. They stop eating and defend their territories by constant, violent fighting. They herd **harems** of as many as 50 females onto their territories and keep other males away (Fig. 9.33). Only the strongest males can hold territories and breed. The others gather into **bachelor groups** and spend much of their time trying to sneak into harems for a quick copulation. Defending the harem is exhausting

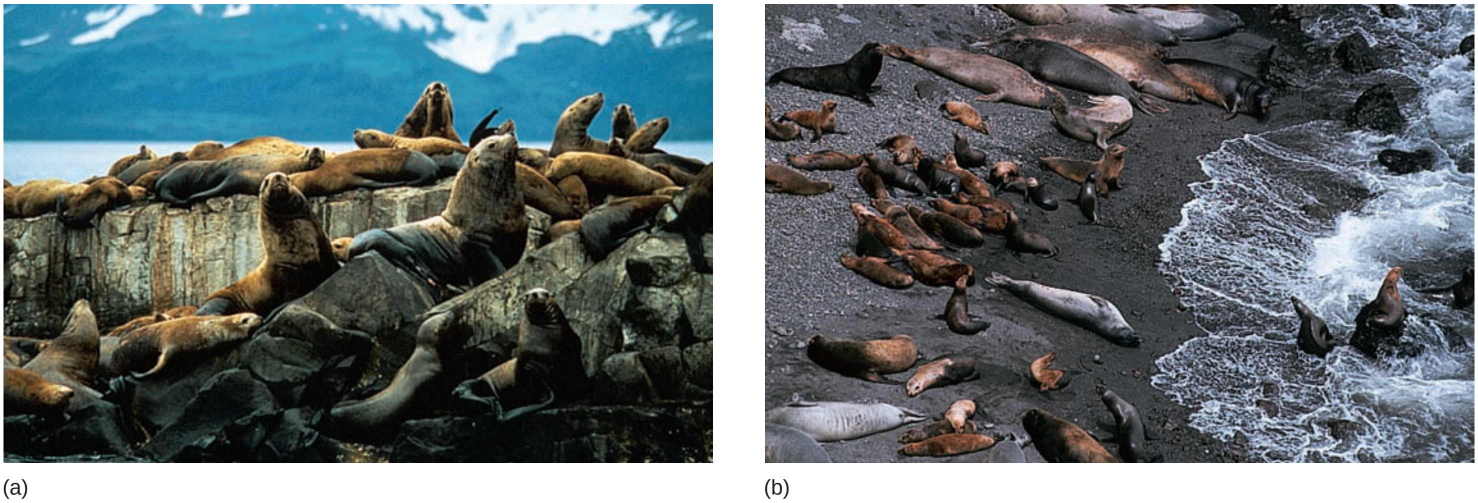

(a) (b)

FIGURE 9.33 (*a*) A male Steller sea lion (*Eumetopias jubatus*) guarding his harem on a rocky island off the coast of Alaska. Steller sea lions are the largest of the eared seals; males may weigh nearly 900 kg (1 ton). (*b*) A harem of female California sea lions (*Zalophus californianus*) on Santa Barbara Island, southern California. The harem (center) is being guarded by a large, darker bull (top left). Large female elephant seals (*Mirounga angustirostris*) rest near the harem, oblivious to the occasional fights between the bull and rival males around the harem.

work, and dominant males "burn out" after a year or two, making way for newcomers. It nevertheless pays off in the huge number of offspring they leave, compared with the males that never reach dominance, even though the subordinate males live longer.

Female pinnipeds give birth to their pups on shore. They seem to be indifferent to the birth process but soon establish a close relationship with the pup (Fig. 9.34). Because females continue to go to sea to feed, they must learn to recognize their own pups out of all the others by sound and smell. The pups generally cannot swim at birth. They are nursed for periods of four days to two years, depending on the species. Most pinnipeds have two pairs of mammary glands that produce a fat-rich milk ideal for the rapid development of the pup's blubber.

A female pinniped can become pregnant only during a brief period after **ovulation,** the release of an egg by her ovaries. This occurs just days or weeks after the birth of her pup. Females of most species return to the breeding grounds only once a year. By contrast, **gestation,** the length of time it takes the embryo to develop, is less than a year. This difference would cause the pup to be born too early, before the mother returns to the breeding ground. To prevent this, the newly formed embryo stops developing and remains dormant in the female's womb, the **uterus.** After a delay of as long as four months, the embryo finally attaches to the inner wall of the uterus and continues its normal development. This phenomenon, known as **delayed implantation,** allows pinnipeds to prolong the embryo's development so that the timing of birth coincides with the female's arrival at the safety of shore.

Delayed implantation allows pinnipeds to time the birth of pups with the arrival of pregnant females in breeding areas.

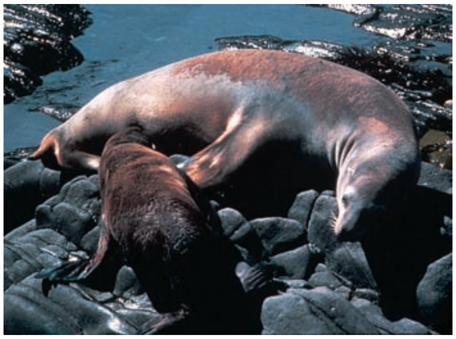


FIGURE 9.34 A California sea lion (*Zalophus californianus*) with a nursing pup.

We know relatively little about cetacean reproductive behavior. We do know that cetaceans are intensely sexual animals. Sex play is an important component of the behavior of captive dolphins. Like humans, they appear to use sex not only for procreation but for pleasure as well. Cetaceans reach sexual maturity relatively early, at age 5 to 10 in great whales. Sexual behavior appears to have a role in the establishment and maintenance of bonds among all individuals, not just potential mates. The sexes are typically segregated within the pod, and males perform elaborate courtship displays to catch the attention of potentially receptive females. Fights among rival males are common, but cooperation also occurs sometimes. Gray whales are known to copulate with the help of a third party, another male that helps support the female (Fig. 9.35*a*). Group matings have been observed in humpback and beluga whales. Considerable touching and rubbing is known to precede copulation (Fig. 9.35*b*). Actual copulation lasts less than a minute but is repeated frequently.

Gestation lasts for 11 or 12 months in most cetaceans. An exception is the sperm whale, which has a gestation period of 16 months. Development in most species of large baleen whales is relatively fast for a mammal of their size. It is synchronized with the annual migration to warm waters. It is remarkable that it takes 9 months for a 3 kg (7 lb) human baby to develop, but a 2,700 kg (3 ton) blue whale calf needs only about 11 months.

Cetacean calves are born tail-first (Fig. 9.36). This allows them to remain attached to the placenta, which provides oxygenated blood from the mother, for as long as possible to prevent oxygen deprivation. The calf immediately swims to the surface. In captive dolphins, the mother or an attending female may help the calf to the surface. Fat-rich milk is responsible

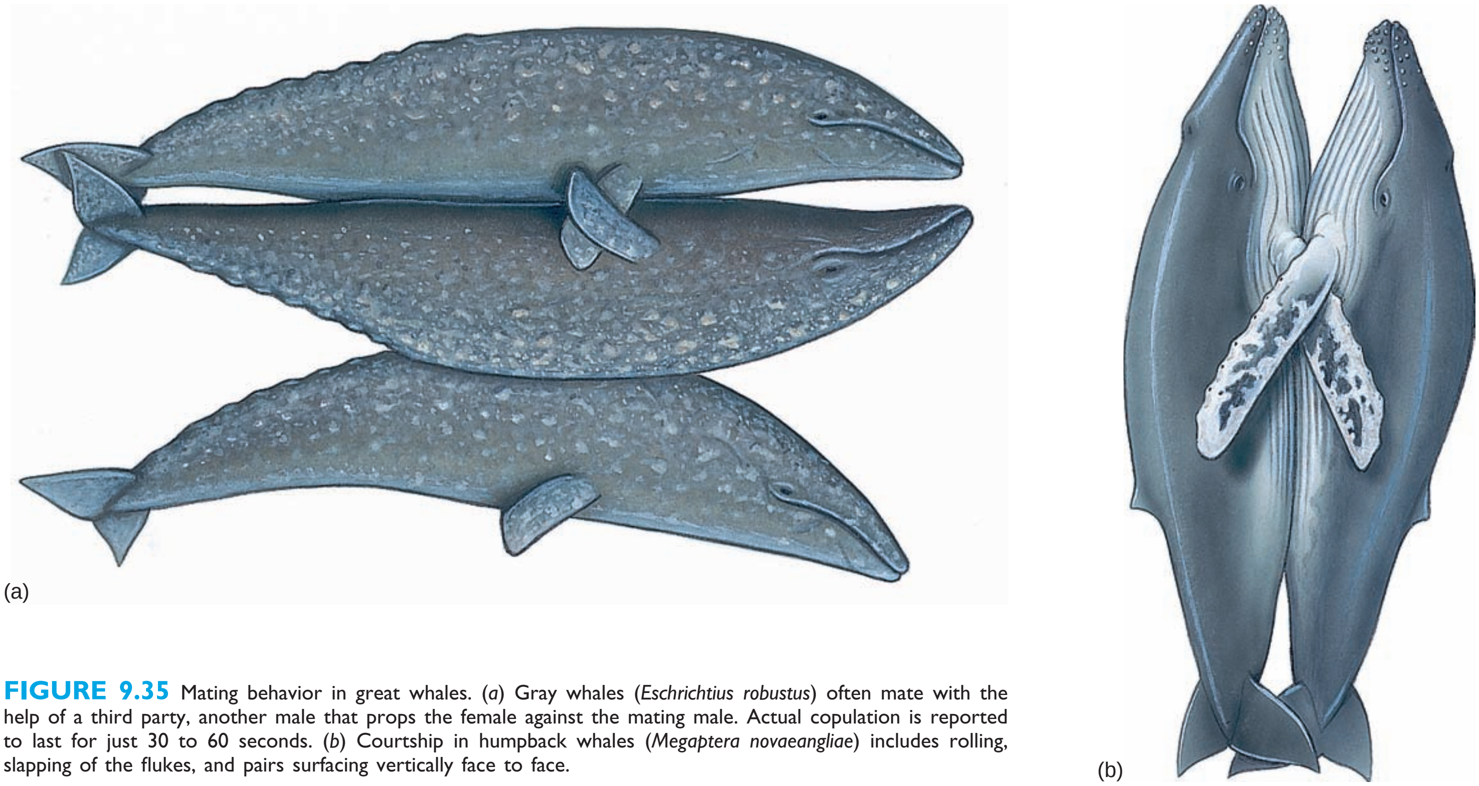


FIGURE 9.35 Mating behavior in great whales. (*a*) Gray whales (*Eschrichtius robustus*) often mate with the help of a third party, another male that props the female against the mating male. Actual copulation is reported to last for just 30 to 60 seconds. (*b*) Courtship in humpback whales (*Megaptera novaeangliae*) includes rolling, slapping of the flukes, and pairs surfacing vertically face to face.

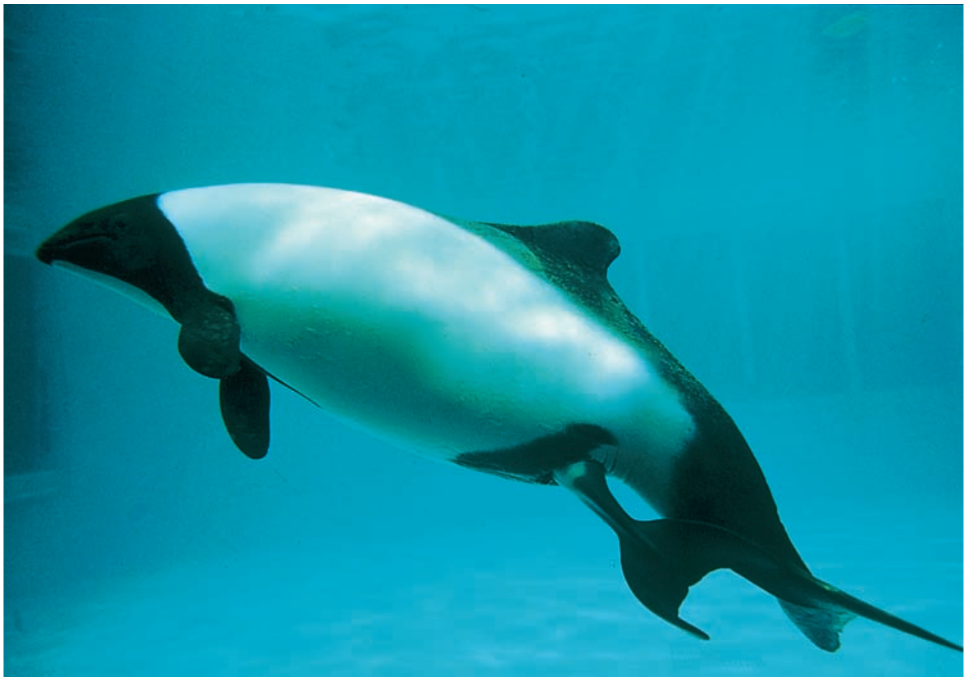


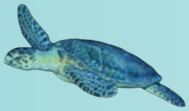
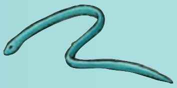
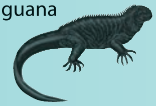
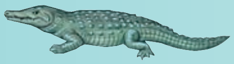
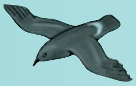
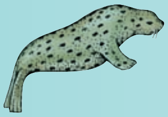
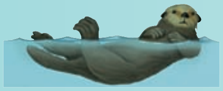
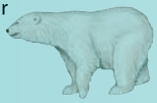
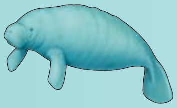
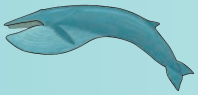
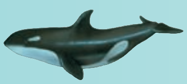
FIGURE 9.36 A Commerson's dolphin (*Cephalorhynchus commersoni*) giving birth in captivity. Not much is known about this dolphin, which is found only in southern South America.

for the rapid growth of calves, particularly in the great whales. They are born without their full complement of blubber and must gain weight before migrating with their mothers to feeding grounds in polar waters. It has been estimated that a blue whale calf gains 90 kg (200 lb) in weight and 4 cm (1.5 in) in length every day for the first seven months of its life. The mother's milk is produced by two mammary glands with nipples located on both sides of the genital slit (see Fig. 9.15). The milk is squirted into the calf's mouth, which allows the calf to drink under water. In at least some of the great whales, females do not seem to feed much while they are nursing. The calves are not weaned until they arrive at the feeding grounds. In some species they continue to nurse for more than a year after birth.

The relationship between mother and calf during the nursing period is very close. Frequent contact and vocalizations are used in communication. Mother whales are known to defend their calves when there is danger. There is a report of a female gray whale lifting her calf onto her flipper to save it from the attacks of killer whales. The bond between mother and calf probably lasts for several years. Captive young dolphins are known to return to their mothers for comfort in times of danger or stress.

Great whales have been estimated to live at least 30 to 40 years on average. Humpbacks are known to live at least 50 years, bowheads 150 years.

Table 9.3 Most Important Characteristics of the Marine Reptiles, Seabirds, and Marine Mammals

Group	Distinguishing Features	Temperature Regulation	Feeding	Reproduction	Significance in the Marine Environment
Sea turtles 	Body covered by shell, scales on exposed parts of body; legs modified as flippers; found mostly in tropical seas	Poikilotherms, ectotherms	Toothless jaws adapted for crushing hard invertebrates or for picking soft invertebrates	Oviparous, laying eggs in sand on land	Predators of jellyfishes and bottom invertebrates; grazers of seagrasses and seaweeds
Sea snakes 	Skin with scales, no legs, laterally flattened for swimming; venomous; found in tropical Indian and Pacific oceans	Poikilotherms, ectotherms	Small teeth adapted for capturing small prey	Ovoviviparous, giving birth at sea, or oviparous, laying eggs on land	Predators of bottom fishes; some feed mostly on fish eggs
Marine iguana 	Skin with scales, tail laterally flattened for swimming; found only in the Galápagos Islands	Poikilotherms, ectotherms	Three-cusped teeth adapted for grazing	Oviparous, laying eggs in nest on land	Grazer of seaweeds
Saltwater crocodile 	Skin with scales, massive jaws and tail; found in coastal regions in Australia, Southeast Asia, and some western Pacific islands.	Poikilotherms, ectotherms	Heavily toothed jaws for capturing wide range of prey	Oviparous, laying eggs in nest of mud and vegetation on land	Predator of wide variety of coastal animals, including fishes, seabirds, sea turtles, crabs
Seabirds 	Feathers for insulation, webbed feet, light bones as adaptation for flight; found in all coastal regions	Homeotherms, endotherms	Beaks adapted for capturing wide range of prey, including filtering	Oviparous, laying eggs in nest on land	Predators of fish and many groups of shallow-water invertebrates, including plankton
Pinnipeds 	Seals, sea lions, walrus: blubber, flippers; found mostly in temparate and polar waters	Homeotherms, endotherms	Teeth for capturing and eating prey	Viviparous, giving birth on land	Predators of mostly fishes; crab-eater seal filters water for krill, leopard seal hunts mostly seabirds, walrus feeds on clams and bottom invertebrates
Sea otter 	Dense, dark fur, dorsoventrally flattened tail, flattened hind feet; found only in northern and northeastern Pacific Ocean	Homeotherms, endotherms	Flattened teeth for capturing and crushing prey	Viviparous, giving birth at sea or on land	Predators of sea urchins and wide range of bottom invertebrates and fishes in kelp forest
Polar bear 	Dense, white fur; found in Artic region, mostly on drifting ice	Homeotherms, endotherms	Powerful jaws and teeth for capturing and eating prey	Viviparous, giving birth on land	Predators of seals
Sirenians 	Manatees, dugong: blubber, reduced hair, front flippers, paddle-shaped tail; tropical seas (one species only in fresh water)	Homeotherms, endotherms	Thick ridge pads for crushing vegetation	Viviparous, giving birth at sea	Grazers of seagrasses and other coastal vegetation
Baleen whales 	Blubber, streamlined body, reduced hair, front flippers, tail fluke, blowhole; found in all seas	Homeotherms, endotherms	Baleen on upper jaw for filtering food	Viviparous, giving birth at sea in warm waters	Filter feeders of plankton and small fishes, mostly in polar waters; gray whale feeds on small animals (mostly amphipods) in soft bottoms
Toothed whales 	Blubber, streamlined body, reduced hair, front flippers, tail fluke, blowhole; found in all seas (some dolphins live in fresh water)	Homeotherms, endotherms	Conical teeth for capturing prey	Viviparous, giving birth at sea	Predators of fishes, squids, and some large bottom invertebrates such as lobsters

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Sea turtles have disappeared from many regions, and one way of trying to save them is to reintroduce them to areas where they have been wiped out. This is done by reburying eggs or by releasing newborn baby turtles on beaches. Why are eggs reburied or baby turtles released instead of fully grown individuals?
2. Most seabirds are specialists that feed on particular types of fish and other prey. In some cases this may reduce the chances of competing with other species of seabirds for limited resources. Sometimes, however, two or more species of seabirds feed on the same type of fish. What type of mechanisms might have evolved to prevent direct competition?
3. Cetaceans give birth to few well-developed calves at well-spaced intervals. They also feed and protect the calves for long periods. This is in sharp contrast to most fishes, in which many eggs are spawned and the parents spend no time feeding and protecting the offspring. What do you think is the best strategy? Has this strategy paid off in the great whales?

For Further Reading

Some of the recommended reading here may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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Coghlan, A., 2006. Whales get emotional. *New Scientist,* vol. 192, no. 2580, December 2–8, pp. 6–7. Certain brain cells linked with intelligence in humans and apes have been found in whales.

Harden, B., 2004. Wild ones. *Discover,* vol. 25, no. 4, April, pp. 52–59. Killer whales are feeding more on protected seals, sea lions, and sea otters, perhaps as a result of a decline in the number of fish.

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Nicklen, P. and K. Heacox, 2006. Deadly beauty. *National Geographic,* vol. 210, no. 5, November, pp. 68–91. The Antarctic leopard seal, in contrast to other seals, feeds almost exclusively on warm-blooded prey.

Palmer, S., 2006. The incredible shrinking iguana. *New Scientist,* vol. 190, no. 2952, May 20–26, pp. 48–49. The marine iguana changes its size, depending on temperature.

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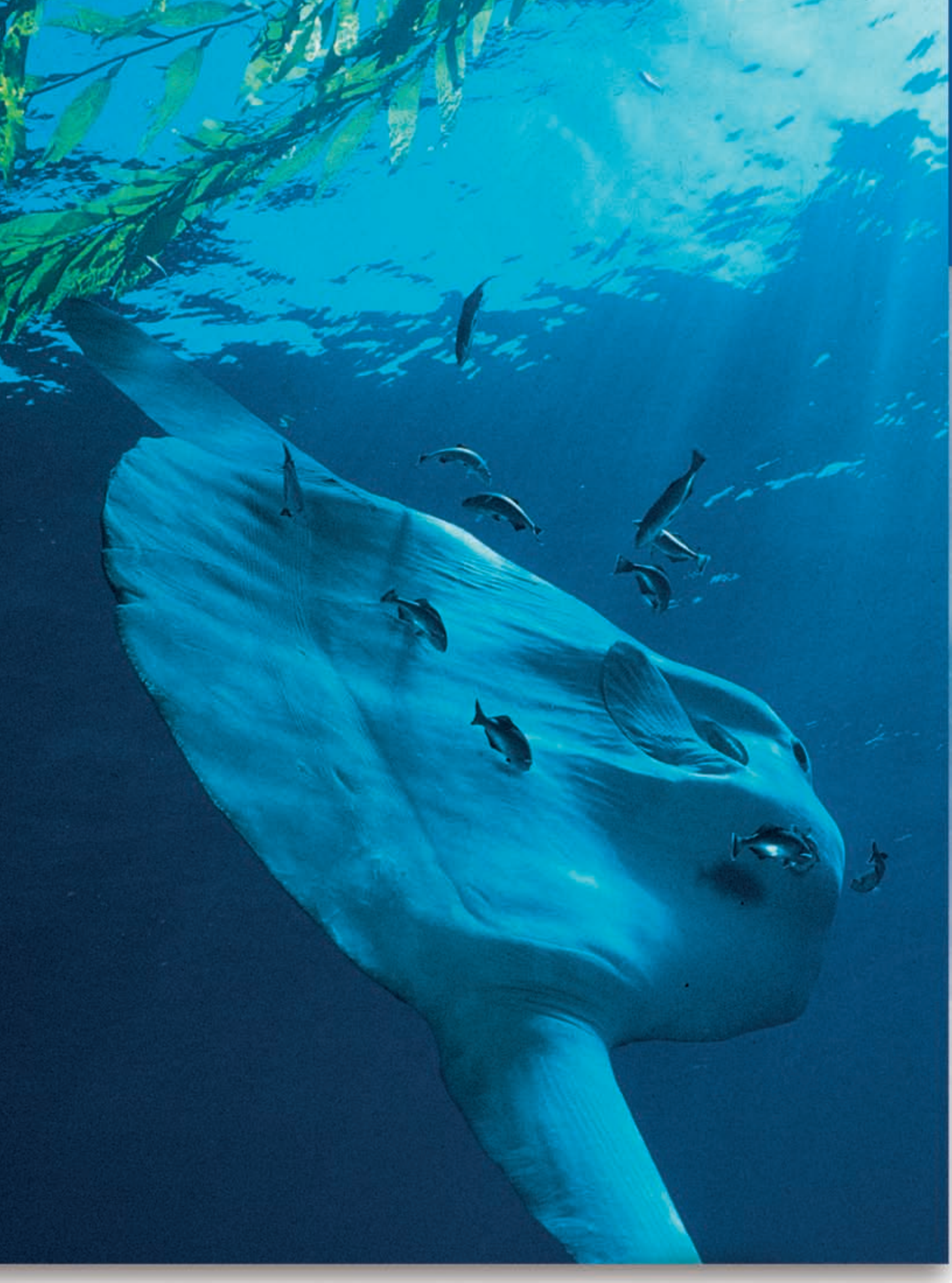
Part Three

Structure and Function of Marine Ecosystems

10

CHAPTER

An Introduction to Marine Ecology



Juvenile halfmoon fish (*Medialuna californiensis*) pick parasites from the skin of an ocean sunfish (*Mola mola*) sheltering under floating kelp fronds.

Everywhere you look in the ocean there are living things. How many and what kind of organisms there are depend on where you go—that is, on the specific nature of the **habitat.** Every habitat has distinct characteristics that help determine which organisms live there and which do not. The amount of light, for example, determines whether algae and plants can grow. The type of bottom, the temperature and salinity of the water, waves, tides, currents, and many other aspects of the environment profoundly affect marine life. Some of these physical and chemical features were introduced in Chapters 2 and 3.

Equally important are the ways that organisms affect each other. They eat each other, crowd each other out, provide habitat for other organisms, and even cooperate. Living things interact in complex and fascinating ways. Part Two of this book, Chapters 5 through 9, introduced the organisms that live in the sea. This part, Part Three, looks at how these organisms live and interact. We will explore the different habitats that make up the ocean world, from the water's edge to the darkest depths. We will consider the special physical and chemical features of each habitat, how the organisms have adapted to each environment, and how they affect each other.

Habitat The natural environment where an organism lives.
- Chapter 2, p. 19

Here in Chapter 10 we first introduce a few basic principles that apply to all habitats. No matter where you go, for instance, algae and plants need light and animals need food. These are just two examples of the interactions among organisms and their environment. The study of these interactions and how they affect the abundance and distribution of organisms is called **ecology.** It is important to realize that ecology is a science, the branch of biology that studies how and why organisms interact with each other and with their environment. Contrary to the way the term is often used in the media, ecology is not the same as protecting the environment, as important as that may be.

THE ORGANIZATION OF COMMUNITIES

The nature of life in a particular habitat is determined to a large extent by the non-living, or **abiotic,** part of the environment, that is, the environment's physical and chemical features such as salinity or bottom type. Each environment has different characteristics that present both challenges and opportunities for the organisms living there.

Organisms are also affected by other organisms—the living, or **biotic,** environment. Biological **populations** interact in complex ways that make the organisms in a **community** dependent on each other.

The nature of a community is determined by both biotic, or living, and abiotic, or non-living, factors.

Organisms must adapt to both the biotic and abiotic features of their environment. Individual organisms can adapt to varying degrees by changes in behavior, metabolism, or other characteristics. Individual seagrasses, for example, adapt to low light levels by an increase in **chlorophyll** content, making them more efficient at capturing what little light *is* available, while corals often adapt through their growth form (Fig. 10.1). In these **physiological adaptations** the genes of the individual organism are unchanged, and the adaptation is not passed on to its offspring. By contrast, genetic differences that make some individuals better adapted to the environment *are* passed on to these individuals' offspring. Over generations, species adapt to the environment through **natural selection** for such advantageous characteristics, a process known as **evolutionary adaptation.**

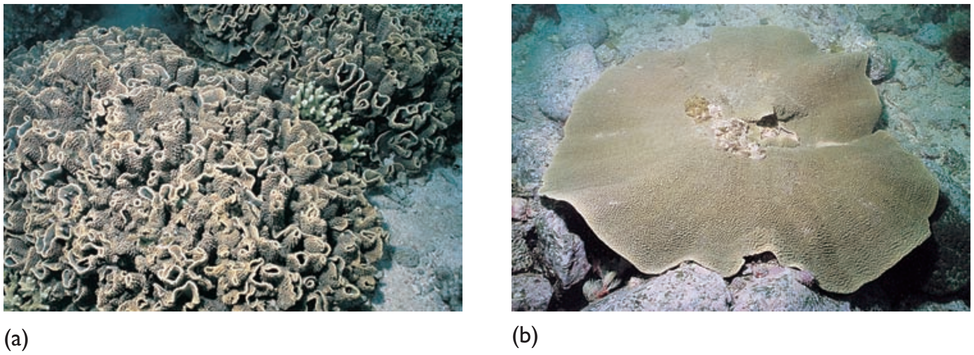

(a) (b)

FIGURE 10.1 These two corals belong to the same species, *Turbinaria mesenterina.* (*a*) The "normal" growth form occurs in relatively shallow water, where there is plenty of light. (*b*) In deeper water, with less light, the coral grows in a flattened shape. This flat shape, like that of a solar panel, is an adaptation that increases the coral's ability to capture the sunlight it needs to grow (see "Light and Temperature," p. 308). This variation in form reflects an individual colony's response to light, and not genetic differences among colonies: The offspring of both colonies will be able to grow in either form depending on light level.

How Populations Grow

When conditions are right, organisms can produce many more offspring than it takes to just replace themselves. If every individual has more than one offspring—or each pair has more than two—the total number of offspring increases every generation (Fig. 10.2). The population grows faster and faster, and there is a population "explosion." Were its reproduction left unchecked, any species could grow to cover the earth in a relatively short time.

Fortunately, we are not up to our necks in dinoflagellates. Though many organisms occasionally undergo dramatic population explosions (Fig. 10.3), reproduction obviously does not continue unchecked forever. Many factors can control, or regulate, the growth of populations. For one thing, explosive population growth can occur only under favorable conditions. When the abiotic environment changes, the population may stop growing or even decline. Some environmental fluctuations, like the seasons, are regular and predictable. Algal growth in temperate and polar regions, for example, often slows dramatically in the winter because there is less light for photosynthesis. Other changes, like a sudden storm or a drifting log that smashes organisms on a rocky shore, are not so predictable. Predictable or not, large or small, changes in the environment can slow the growth of or even wipe out populations. Of course, conditions that wipe out one species might be just right for another.

There are also mechanisms that limit population growth even if the non-living environment doesn't fluctuate. Some animals slow down or stop reproduction when their habitat becomes too crowded. Others fight among themselves or even cannibalize each other. Natural enemies may be attracted when the population gets large, or diseases may spread faster under crowded conditions. Large populations can pollute the environment with their own wastes.

As more and more individuals join the population, they use up their **resources,** the things they need to live and reproduce, like food, **nutrients,** and living space. Eventually there are just not enough resources to support any more individuals and the population levels off (Fig. 10.4). The largest population size that can be sustained by the available resources is called the **carrying capacity.**

Organisms use many different resources. A lack of any one of these will slow or prevent growth and reproduction. A dinoflagellate living in the open ocean, for example, can be limited by a lack of nitrate (NO_3^{-1}), even if it has plenty of light, water, carbon dioxide (CO_2), and nutrients other than nitrate. During the winter in polar regions, there may be plenty of nitrate but not enough light. Seaweeds on a rocky shore, on the other hand, might have plenty of light and nutrients but be unable to grow because there is no space left. A **limiting resource** is one whose short supply restricts the growth of a population.

Because of the drain of resources or other effects of crowding, populations do not grow forever. As the population becomes more crowded, its *growth rate* goes down. In this sense the population is **self-regulating;** that is, its growth rate depends on its own numbers. Whereas non-living factors such as the weather can affect populations of any size, self-regulation acts only when the population is large.

Populations are capable of explosive growth. Population growth is usually limited, however, by either the non-living environment or by the activities of the organisms themselves.

As resources are depleted, there are not enough to go around. Each individual has to vie with other organisms for what resources remain. **Competition** is the interaction that results when a resource is in short supply and one organism uses the resource at the expense of another (Fig. 10.5). When members of the same species compete it is called **intraspecific competition.**

Those who compete successfully survive to replace themselves by reproducing. The poorer competitors do not reproduce as successfully and eventually disappear. Nature thus favors the members of the population that are best suited to the environment. Because of this natural selection, the population as a whole is, on average, a little better adapted each generation. In other words, the population **evolves.**

Ways That Species Interact

Species do not live in a vacuum, isolated from other species. Members of different species may have strong effects on each other. Species can interact in many ways, all of which influence the organization of communities.

Population A group of individuals of the same species that live together.
Community All the different populations of organisms that live in the same place.
- Chapter 4, p. 71

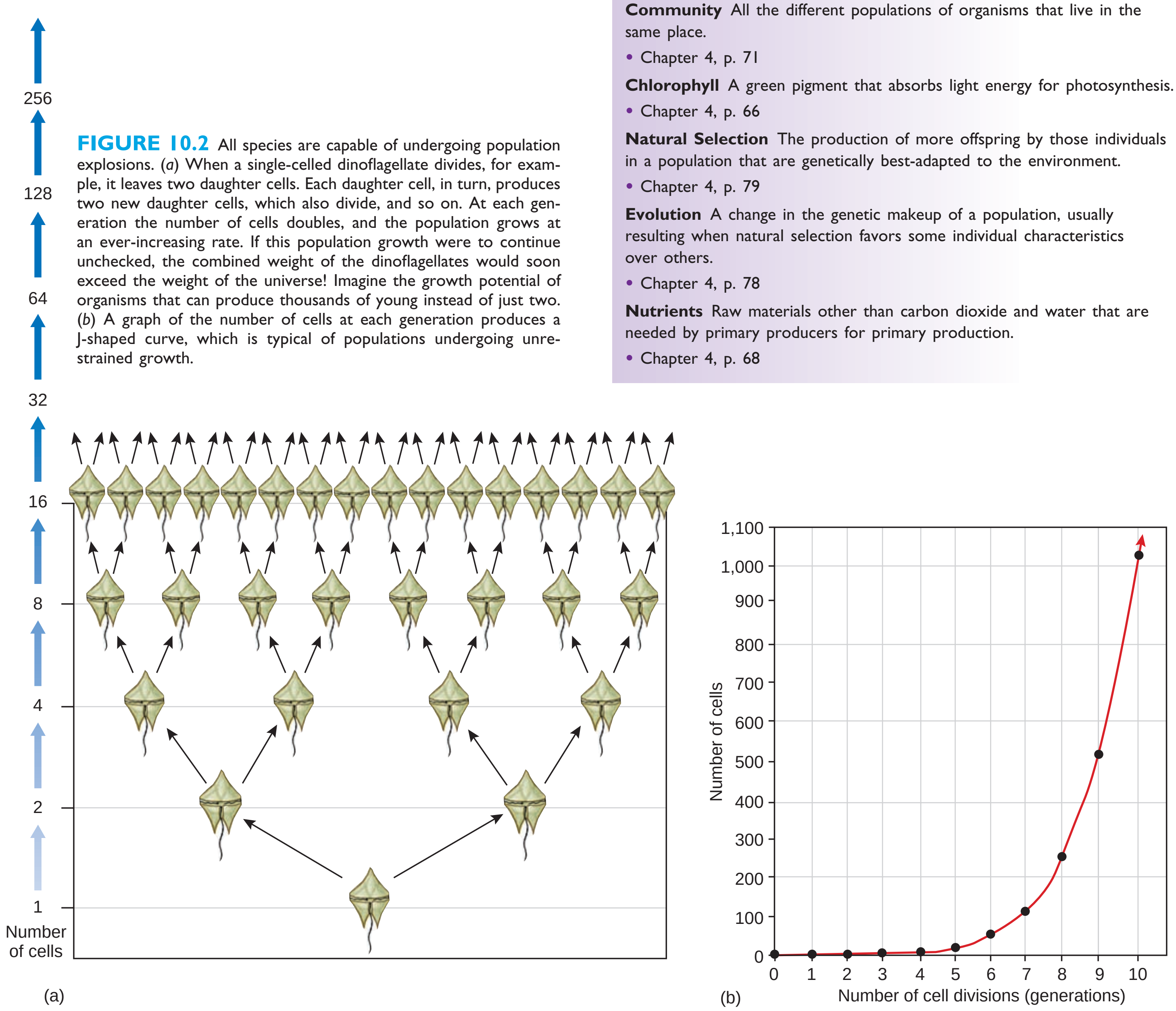
Chlorophyll A green pigment that absorbs light energy for photosynthesis.
- Chapter 4, p. 66

Natural Selection The production of more offspring by those individuals in a population that are genetically best-adapted to the environment.
- Chapter 4, p. 79

Evolution A change in the genetic makeup of a population, usually resulting when natural selection favors some individual characteristics over others.
- Chapter 4, p. 78

Nutrients Raw materials other than carbon dioxide and water that are needed by primary producers for primary production.
- Chapter 4, p. 68

FIGURE 10.2 All species are capable of undergoing population explosions. (*a*) When a single-celled dinoflagellate divides, for example, it leaves two daughter cells. Each daughter cell, in turn, produces two new daughter cells, which also divide, and so on. At each generation the number of cells doubles, and the population grows at an ever-increasing rate. If this population growth were to continue unchecked, the combined weight of the dinoflagellates would soon exceed the weight of the universe! Imagine the growth potential of organisms that can produce thousands of young instead of just two. (*b*) A graph of the number of cells at each generation produces a J-shaped curve, which is typical of populations undergoing unrestrained growth.



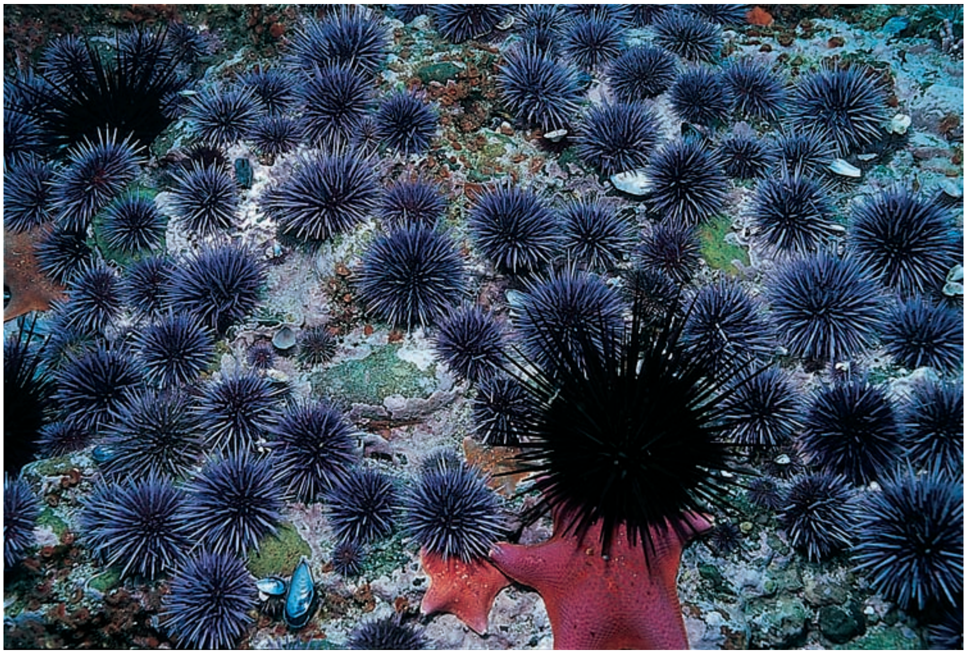


FIGURE 10.3 The purple sea urchin (*Strongylocentrotus purpuratus*) from the Pacific coast of North America sometimes undergoes dramatic population explosions, as do many other urchin species. The outbreaks can have dramatic effects on the rest of the community. This photo also shows a few individuals of the larger red urchin (*S. franciscanus*), which in this photo look black.

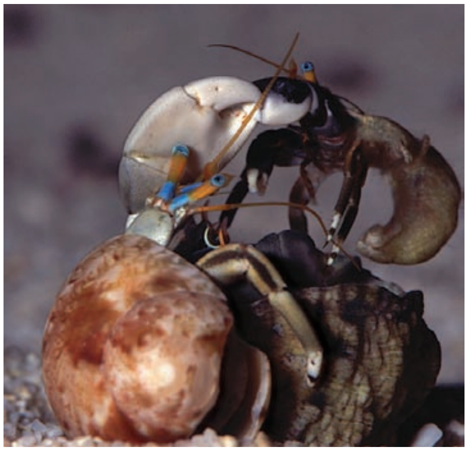


FIGURE 10.5 The short supply of any resource can lead to competition. Hermit crabs rely on abandoned snail shells for protection. When they grow out of their old shell or it wears out they must move into a new shell, and sometimes there aren't enough shells to go around. These left-handed hermit crabs (*Calcinus laevimanus*) are fighting over a shell they both want. The one on the left has evicted the one on top from its shell and will take the shell over.

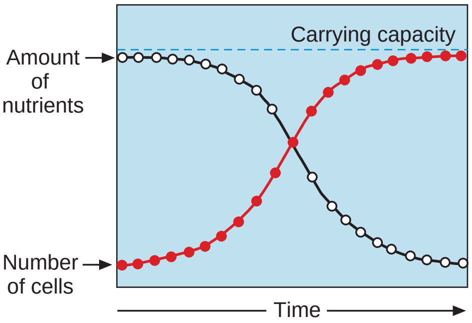


FIGURE 10.4 The kind of explosive population growth shown in Figure 10.2 would never go on forever. As the dinoflagellates get more and more numerous, they use up the nutrients and other resources that they need to grow and reproduce. The maximum number of cells that the nutrient supply can support is called the carrying capacity of the system. Curves like this are often observed in laboratory experiments, but in the real world they are rarely so smooth.

Competition Organisms must compete for resources not only with members of their own species, but with members of other species. Competition between species is known as **interspecific competition.**

When two species use the same resource and the resource is scarce, the species must compete just as if they were members of the same population. One of the two species usually turns out to be better at the competition. If two species eat exactly the same food, for example, one of the two will be better at catching it. Unless something interferes, the inferior competitor loses out and the competitively superior species takes over. When one species eliminates another by outcompeting it, **competitive exclusion** is said to occur.

Competition between species results when both species use a scarce resource. In competitive exclusion, one species wins the competition and eliminates the other from the community.

Sometimes a competitively superior species is prevented from excluding poorer competitors. Periodic disturbances such as severe storms, battering by drifting logs, or underwater landslides can reduce the population of a dominant competitor and give other species a chance (see Fig. 11.24). Furthermore, which species is competitively superior sometimes depends on the conditions. On rocky shores in tropical Hong Kong, for example, foliose (leaf-like) algae (*Dermonema, Pterocladia*) are the dominant seaweeds during the relatively cool winter. In the summer heat these forms die out and are replaced by more resistant encrusting algae (*Ralfsia*). Seasonal variation thus prevents either group from excluding the other and there is a shifting balance between competing species.

Species can also avoid excluding each other if they share the limiting resource, with each species specializing on just part of the resource. For example, two species of fish that eat seaweeds might divide the resource by specializing on different kinds of seaweed. Animals that eat exactly the same thing might live in different places or feed at different times, staying out of each other's way. Ecologists call this sharing of a resource by specialization **resource partitioning.**

Species that might otherwise competitively exclude each other sometimes coexist by resource partitioning, or dividing the resource.

Biodiversity: All Creatures Great and Small

From bacteria to baleen whales, our planet is home to tens of millions of life forms at least; biologists can only guess at the true number of species. The richness and variety of life is referred to as **biological diversity,** or just **biodiversity.** In recent years biodiversity has been the focus of discussion not only in scientific circles but in the news media and the highest levels of government and international affairs. The reason for this attention, unfortunately, is that the earth's biodiversity is disappearing. Extinction is a natural event that has gone on since life first appeared on earth, but pollution, habitat destruction, overexploitation, and other human folly are now driving species extinct at a rate unprecedented in the history of life. At the rate things are going, most kinds of living things will disappear forever from the face of the earth, many before we even know they are there.

When it comes to conservation, the emphasis of decision makers, conservation organizations, and the general public has traditionally been on organisms that we find beautiful or emotionally compelling. Bald eagles, whales, and redwood trees evoke strong, positive reactions in most people; microscopic worms and bottom-dwelling fungi do not. Worms, fungi, and millions of other seemingly insignificant species are at least as vital to earth's survival—and therefore to our own—as are the larger organisms that we happen to find attractive. There is a growing recognition of the need to protect the earth's biodiversity, to reverse or at least slow the process of mass extinction. What is new about this is a focus on maintaining the total *number* of species, rather than on saving particular ones.

So why should we care about how many different *kinds* of organisms there are, as long as the ones we care about are still around? For one thing, no organism lives in isolation from its environment and the other living things in it. Creatures like whales, pandas, sea turtles, tigers, and other "flagship species" cannot survive without countless other species. Organisms are bound together in complex food webs, nutrient cycles, symbioses, and other ecological interactions. The loss of even the "lowliest" of species could have profound effects on many others. Biologists simply do not understand ecosystems well enough to predict what these effects might be.

Another reason to conserve biodiversity is that it represents a hidden treasure trove. Most pharmaceuticals are derived from natural chemicals in organisms, but only a tiny fraction of species have been tested. The wild plants from which our farm plants were derived contain genes for pest resistance, faster growth, and higher quality that could be used to improve our food crops or develop new ones. New materials—a substitute for petroleum, perhaps, or industrial chemicals or better fibers for clothing—also remain undiscovered. There are so many different kinds of organisms that scientists have not had time to even identify most of them, much less evaluate their usefulness. The next species that goes extinct might hold the cure for cancer, a solution to hunger, or maybe just the makings of an elegant new perfume—a secret that will be lost forever.

There is also growing evidence that having a lot of different species is a good thing in and of itself. A diverse community, one with a lot of species, seems to be more efficient at using the available resources than one that is less diverse. A diverse community produces more food and oxygen, breaks down waste faster, and is more likely to survive a natural disaster. Diverse communities also seem to be more resilient both to natural disturbances such as disease outbreaks or extreme climatic events and to human disturbances including pollution, fishing pressure, and the introduction of alien species. The loss of species may be placing ecosystems in greater and greater jeopardy, not only because of the value of particular individual species but also because having a lot of species, whichever ones they are, is important. Humans, having become a largely urban species, sometimes forget that our survival still depends on natural ecosystems to produce oxygen, clean water, and much of our food and materials; to process our wastes; and even to maintain our climate.

What can be done? Some scientists fear that it is already too late, that the planet is irreversibly headed for disaster. Others are more optimistic, but all agree that we should at least try to maintain the earth's biodiversity. Governments and decision makers have begun to listen. At the 1992 Earth Summit in Rio de Janeiro, world leaders from nearly all countries gathered to discuss the critical environmental issues that threaten the planet, and therefore the well-being of people. A major result of the conference was the **Convention on Biodiversity.** Participants agreed that protecting diversity requires finding ways for poor countries to develop economically without destroying their natural biodiversity, a concept dubbed "sustainable development." This, in turn, will require developed countries to make a major commitment to scientific research and technical assistance to developing countries. Some important steps have already been taken, such as setting up global programs to monitor the health of the oceans, assist sustainable development projects, and reduce pollution. At the World Summit on Sustainable Development in 2002, governments agreed to a target of "significantly reducing" the rate of biodiversity loss by 2010. This is an ambitious target, but what is "significant" is not defined, scientists have not yet been able to actually measure how fast biodiversity is disappearing, and so far, governments have not really put their money where their mouths are and committed the funding needed to reach the target. Preserving the earth's biological heritage from the ravages of our activities will be a challenge for people, and their governments, everywhere. We can only hope that it is not insurmountable.

Resource partitioning allows species to coexist when they might otherwise exclude each other, but it does have its price. By specializing, each species gives up some of the resource. The fish that specializes on just one kind of seaweed, for example, will have less food available than if it ate all types. With fewer resources available, the size of the population tends to be smaller. On the other hand, the species might be able to use the resource more efficiently by being a specialist than if it were a "jack-of-all-trades." Different species of shorebirds, for example, have specialized bill shapes that make them more efficient at feeding on particular types of mudflat animals (see Fig. 12.12) and may also reduce competition. Not all specializations, however, are a result of interspecific competition (Fig. 10.6).

To be successful in the long run, a species must find the right balance between specialization and generalization. There is no one best answer to the problem—just look at all the different kinds of organisms. Each species has its own special role, or **ecological niche,** in the community. A species' niche is defined by the combination

EYE ON SCIENCE

The Census of Marine Life

Growing concern about the loss of biodiversity has made marine biologists painfully aware of how little they really know. Less than 1% of the oceans has been explored, and millions of marine species have yet to be discovered. The species that have are still largely a mystery—we know little about their abundance and geographic distribution, much less their ecology or how humans are affecting them. To assess marine biodiversity and set conservation targets we need to know much more. In 2000 scientists embarked on a decade-long Census of Marine Life (COML), asking: What lived in the oceans before humans began altering marine ecosystems? What lives there now? and What will live in the oceans in the future?

COML encompasses all parts of the ocean and all its organisms, and could never be accomplished by a single team or project. COML is an expanding network of hundreds of scientists in more than 80 countries working on a coordinated set of projects. The History of Marine Animals Project (HMAP), for example, studies what lived in the oceans. One reason this question is important is to avoid the "shifting baseline problem." If a given fish population has crashed, for example, restoring the population to a 1950s level might sound like a reasonable target, but what if the population was already depleted in 1950? The appropriate baseline is the natural population size before human influence, which for most species is unknown. HMAP focuses on fisheries because fishing is the oldest and most intensive human impact in the sea. Historical catch records, genetic analysis, and ecological data like fish scales preserved in sediments are revealing the true extent of human impact. HMAP researchers recently estimated, for example, that the cod population off Nova Scotia has plummeted by 96% since 1850.

COML scientists are also revealing previously unsuspected levels of marine biodiversity. From poles to tropics, deep sea to coastal lagoons, they are discovering dozens of new species a day. The Census is on track to double the number of known zooplankton species, and in 2006 just three cruises to Antarctic waters collected more new species than previously discovered by centuries of explorers. Similar results are being obtained throughout the ocean. The deluge of species new to science looks like it won't abate anytime soon, either. Using genetic barcoding COML researchers can quickly identify species by reading short DNA sequences, and can use novel sequences to estimate numbers of unknown species. In one study, more than half of mantis shrimp larvae collected belonged to species never been recorded as adults. Biologists thought they already knew most mantis shrimp species, and unknown diversity is probably even higher in less well-known groups. It goes through the roof for microorganisms: A single liter of seawater yielded more than 20,000 types of bacteria, most of them new!

The Census is also learning about species we already know. Using revolutionary technology, COML is developing a global Ocean Tracking Network (OTN) that will allow scientists to continuously monitor the movements of more than a million animals whose lives at sea have until now been a mystery. Transmitters, acoustic receivers, and satellites have already been used to track a variety of marine animals, including salmon, tuna, sharks, seals, whales, penguins, and migratory seabirds.

The Ocean Biogeographic Information System (OBIS) will make the vast amount of COML data easily accessible, in a user-friendly way, by developing an online database and pulling together databases that already exist. OBIS already includes more than 10 million distribution records of more than 80,000 species, and is growing at an ever-increasing pace.

When COML finishes in 2010 will we know all there is to know about the oceans? Of course not. But vastly more will be known than when the program started, the information will be readily accessible to all, and great strides will have been made in methods and technologies for exploring marine ecosystems. Just as importantly, we will have a much better idea of what we don't know, and what will ultimately remain unknowable.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

of virtually every aspect of its lifestyle: what it eats, where it lives, when and how it reproduces, how it behaves, and so on.

> The role a species plays in the community is called its ecological niche. The niche includes feeding habits, habitat use, and all the other aspects of the species' lifestyle.

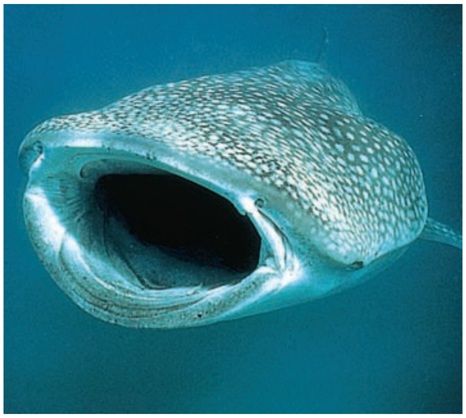


FIGURE 10.6 The whale shark (*Rhiniodon typus*) feeds by straining plankton from huge mouthfuls of water. It has probably evolved a huge mouth and lost the large teeth of most other sharks not to avoid competition with other sharks but as adaptations for efficient plankton feeding.

Predator-Prey Interactions Species don't always compete for resources. Sometimes they use each other as the resource. In other words, they eat each other (Fig. 10.7). **Predation** is the act of one organism eating another. The organism that does the eating is the **predator,** and the organism that gets eaten is the **prey.** The term "predator" is often reserved for **carnivores,** animals that eat other animals. A special case of predation occurs when organisms eat algae or plants. This is usually called **herbivory** rather than predation, and the organism doing the eating is called a **herbivore.** No matter what you call it, the alga or plant gets eaten just the same.

Predation obviously affects the individual organism that gets eaten. It also affects the prey population as a whole by reducing the number of prey. If the predators don't eat too much, reproduction by the prey population can replace the individuals that have been eaten. If predation is intense, however, it can greatly reduce the prey population.

The interaction between predator and prey is not a one-way street. After all, the predator depends on the prey for its food supply. If bad weather or disease wipes out the prey, the predators suffer as well. Prey populations can also decline if there are too many predators or the predators eat too much. In this case the predator population soon starts to decline, having used up its food supply.

Predation, which occurs when an animal eats another organism, affects the numbers of both predator and prey.

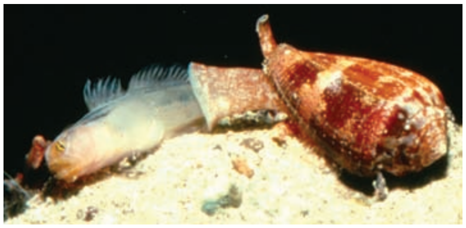


FIGURE 10.7 Predation. A purple cone shell (*Conus purpurascens*) engulfs its prey, a redhead goby (*Elacatinus puncticulatus*). It paralyzed the fish by injecting powerful venom through a hollow, harpoon-like tooth derived from the radula.

Predators often affect species other than their prey. On temperate rocky shores, for example, sea stars that selectively prey on mussels make space for the mussels' competitors, who would otherwise be crowded out (see Fig. 11.22). Feeding, or **trophic,** interactions such as this, in which the effects of one species on another go on to affect a third species, are called **indirect interactions.** Indirect interactions sometimes result in relationships among species that are contrary to what might be expected. On Caribbean coral reefs, for example, a grazing **chiton** (*Choneplax lata*) actually *increases* the abundance of its primary prey, a coralline alga (*Porolithon pachydermum*). The chiton only scrapes a thin layer off the surface of the alga, which not only leaves most of the alga but stimulates its growth. The chiton also removes competitively superior algae that grow faster than the coralline alga. Furthermore, these fast-growing algae attract parrotfish grazers whose deep bites do completely remove the coralline alga. Thus, there is often a web of indirect interactions, which means that an effect on one species may flow through an ecosystem in what is called a **trophic cascade.** In the northwest Pacific, for example, the effects of depleting fishes that are the prey of seals and sea lions flow through to killer whales, otters, sea urchins, and entire kelp beds (see "Kelp Communities," p. 296).

Predator-prey interactions can also cause the effects of physical factors to cascade through a community. For example, a mud snail (*Hydrobia ulvae*) is the main grazer on seagrass **epiphytes** in North Sea seagrass beds. Epiphytes compete with the seagrass for light and nutrients, slowing seagrass growth. Where snail grazing keeps the seagrass leaves clean, the beds grow thick and lush. At exposed sites, however, currents wash the snails away, epiphytes grow in profusion, and the seagrass beds are sparser.

A tremendous variety of predatory strategies have evolved. Sharks and tunas are highly efficient killing machines, swift and powerful. Other predators sneak up on their prey, catching them unaware. Predators such as anglerfishes go a step further and lure their prey. Many snails can drill through their prey's shell, and many sea stars evert their stomachs to digest prey outside their bodies (see "Feeding and Digestion," p. 144). Many predators eat only part of the prey, leaving the rest alive to continue growing. In the following chapters we will examine some of the many ways that predators catch their prey.

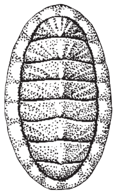
The most successful individual predators catch more food and thus tend to survive longer, grow faster, and produce more offspring. Natural selection, therefore, favors the most efficient predators in the population. Each generation will be a little better at capturing its food.

Natural selection also favors the prey individuals that are most successful at getting away. Organisms have evolved at least as many ways to escape from predators as there are predators. Some are fast and elusive; others use camouflage (Fig. 10.8). Many organisms have protective spines, shells, or other defensive structures. Many seaweeds and animals protect themselves with distasteful or even poisonous chemicals.

Organisms may also take advantage of the defenses of other species. Many sea slugs, or nudibranchs, for example, protect themselves from predators with noxious chemicals or stinging cells that they obtain from their prey (see "Gastropods," p. 129). In North Carolina, a brown alga (*Sargassum filipendula*) competes

Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface.
- Chapter 7, p. 132

Epiphytes Photosynthetic organisms that live on the surface of algae or plants.
- Chapter 5, p. 89



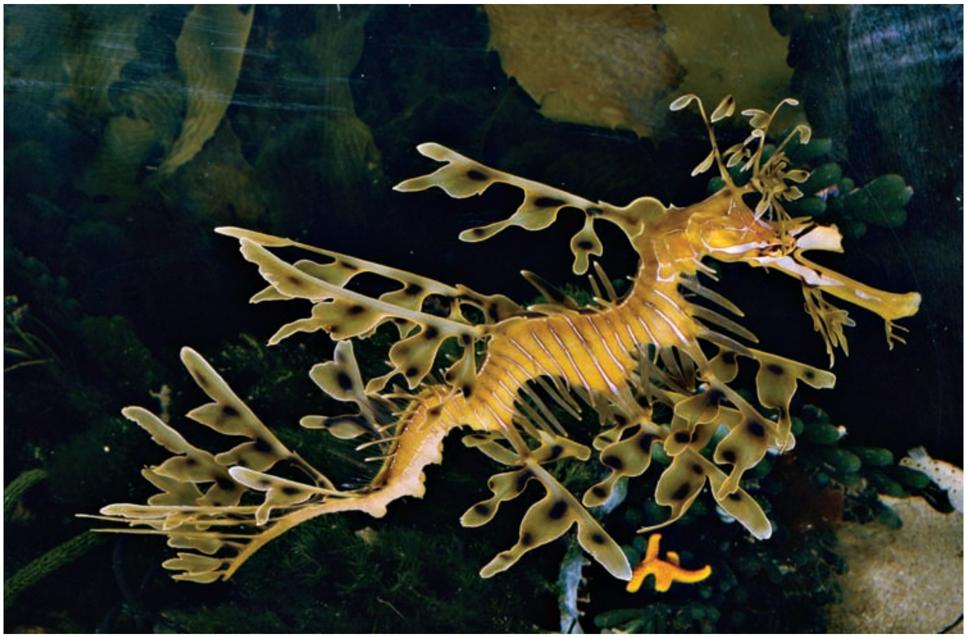
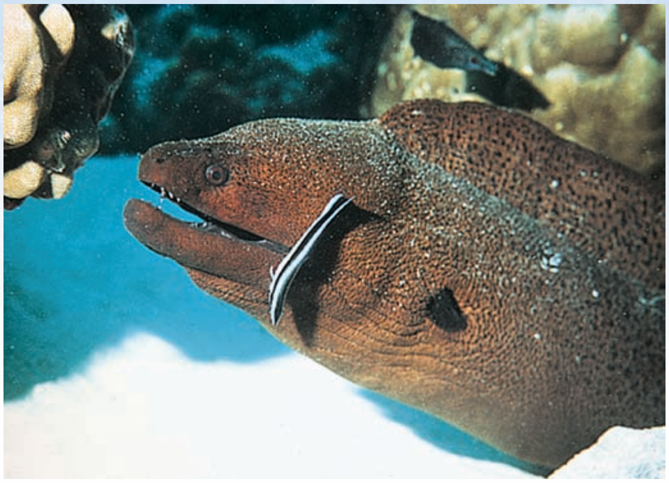


FIGURE 10.8 The frond-like projections of the leafy seadragon (*Phycodurus eques*) make these fish look like a bit of drifting seaweed. Not only does this hide them from sharks and other predators, but it also allows them to sneak up on their own prey, tiny shrimps. They also have sharp, protective spines in case a predator isn't fooled by the camouflage.

Cleaning Associations



A cleaning wrasse (*Labroides*) doing its job on a moray eel (*Gymnothorax*).

Some small fishes and shrimps form **cleaning associations** with larger "clients" in which the cleaner makes a living by picking parasites and dead or diseased tissue off its clients. Cleaner fishes include wrasses, butterflyfishes, and gobies, while the banded coral shrimp (*Stenopus hispidus*) is the best-known cleaner shrimp. Usually the clients are fishes, but octopuses have also been seen to take advantage of the service. Cleaning behavior can be a full- or part-time job. Some species are cleaners all their lives, others only as juveniles. Cleaning associations are especially common in coral reef, kelp bed, and other shallow, hard-bottom communities.

To attract clients, cleaners set up a "cleaning station," usually marked by a prominent feature like a large sponge or conspicuous rock. Cleaners also often have characteristic bright colors and distinctive stripes to advertise their services, which are popular: Clients sometimes have to wait in line. Clients remember where the stations are and continue to visit for a while even after a cleaner is experimentally removed.

Some clients are carnivores that could easily cheat the system and swallow a cleaner in one gulp. Perhaps to signal their good intentions, many clients swim unusually slowly, hovering in midwater. Some change color, or assume unusual postures. Cleaner fishes swim close to the client to inspect it. Some "dance" as part of the ritual, perhaps to remind the host that they are cleaners and not food. Cleaner shrimps use their antennae, tapping the host. Once the cleaning starts, the hosts remain still to allow the cleaners to pick at their skin and fins. They often open their gill covers to allow the cleaner to inspect and clean their gills. The cleaner can even swim inside the mouth without mishap, at least most of the time.

Cleaning associations benefit both sides. The cleaners get a reliable food supply that comes to them, although they are occasionally infected by the very parasites they are trying to eat. Cleaners effectively control their clients' parasites, which presumably benefits the client more in the long term than making the cleaner into an easy meal.

Clients do sometimes cheat the system and eat a cleaner. Cleaners also cheat occasionally, biting off a scale or some protective mucus from a client. Cheating is rare, however, and both sides have strategies to keep the other side honest. Clients will punish cleaners who try to cheat, attacking them or taking their business to a different cleaning station. They will also move on if the cleaner keeps them waiting. It even appears that they watch how cleaners treat other clients and select cleaners that behave cooperatively. There is also evidence that cleaners behave better when they are being watched.

For their part, cleaners learn to recognize individual clients and may reject ones that didn't behave themselves during a previous encounter. They even give preferential treatment to clients that have access to a choice of cleaning stations and might seek better service elsewhere.

Some blennies (*Aspidontus, Plagiotremus*) have color patterns and behavior that mimic local cleaner wrasses. The blennies use this deception to get close to would-be clients, then dart in to take a bite of skin, scale, or fin before dashing to safety.

with a red alga (*Hypnea musciformis*) and slows its growth when the two occur together. Nonetheless, the red alga *only* occurs together with the brown one when grazing fishes are abundant, because the brown alga is unpalatable and helps deter the fishes from eating the red one, which they relish.

Some organisms use their defenses only when they need them. The barnacle *Chthamalus anisopoma* from the Gulf of California, for example, normally grows upright, but when predatory snails are abundant it grows bent over. This makes it more difficult for the snails to get through the covering plates on the barnacles' upper surface. Some algae that use chemical defenses only produce the nasty chemicals after they have been damaged. Thus, they don't waste energy making the chemicals until they are needed. Defense mechanisms that are used only in response to predators are called **inducible defenses.**

Thus, there is a continual "arms race" between predators and their prey. The predator keeps getting better at catching the prey and overcoming its defenses. In response, the prey becomes more adept at escaping or develops better defenses. This interplay, with each species evolving in response to the other, is known as **coevolution.**

Symbiosis Coevolution becomes even more important when species interact more intimately. Members of different species may live in very close association, even with one inside another (see "From Snack to Servant: How Complex Cells Arose," p. 73). Such close relationships are examples of **symbiosis,** which literally means "living together." The smaller partner in the symbiosis is usually called the **symbiont** and the larger one the **host,** though sometimes the distinction is unclear.

Biologists traditionally divide symbiosis into different categories according to whether the organisms involved benefit or suffer from the relationship. In **commensal** relationships, one species obtains shelter, food, or some other benefit without affecting the other species one way or the other. For example, certain barnacles live only on whales (Fig. 10.9). The barnacles get a place to live and a free ride. They feed by filtering the water, and as far as we can tell the whale is neither harmed nor helped by the barnacles. There are many other examples of symbiotic organisms that live on, or even in, a host without apparently either hurting or helping it (see Fig. 7.35).

On the other hand, sometimes the symbiont benefits at the expense of the host (Fig. 10.10). This is called **parasitism.** The giant

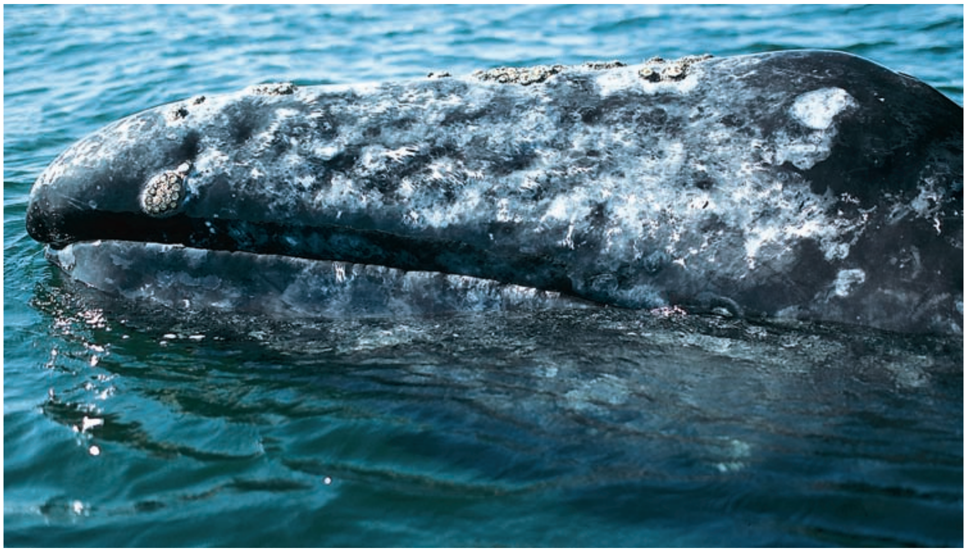


FIGURE 10.9 Some barnacles live only on the skin of whales. Because they do not appear to affect their host at all, most such barnacles are considered to be commensals.

tapeworms that derive food and shelter by living in the guts of whales (see "Flatworms," p. 123) are considered parasites because they may weaken their whale hosts. Marine parasites are very common. In fact, few marine species escape having at least one kind of parasite.

Not all symbiotic relationships are one-sided. In **mutualism,** both partners benefit from the relationship. In many places, small cleaner fishes and shrimps have mutualistic relationships with larger fishes known as **cleaning associations** (see "Cleaning Associations" p. 218).

In the case of cleaning associations, both partners can get by without the other if they have to, which is called **facultative symbiosis.** In **obligate symbiosis** one or both partners depend on the other. In the symbiosis that forms lichens, for example (see "Fungi," p. 99), both the fungus and the alga are obligate symbionts that cannot live without the other.

> In symbiosis, members of different species live in close association. Symbiosis includes parasitism, in which the symbiont harms the host, commensalism, in which the host is not affected, and mutualism, in which both partners benefit.

In practice, it may be very difficult to tell whether the partners in a symbiotic relationship are helped or harmed. Some biologists prefer to emphasize the movement of energy or of food or other materials between the partners, without reference to possible harm or benefit.

Like other interactions among species, symbiosis can have indirect effects. In exchange for shelter and food, in the form of mucus, the colorful crab shown on p. 115 drives away the sea star predators of its coral host. This can protect other nearby corals as well as the host coral, because the sea stars avoid crawling over the host to get to the other corals.

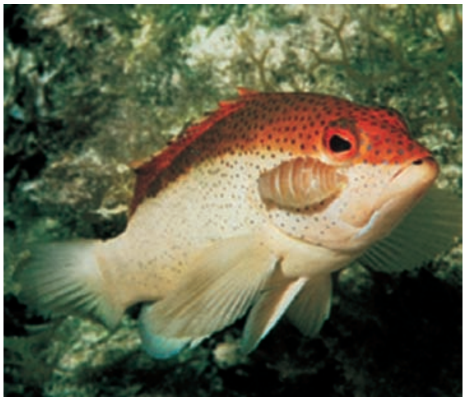


FIGURE 10.10 The isopod (*Anilocra*) just below the eye of this coney (*Cephalopholis fulva*) is a blood-sucking parasite of fishes.

Larval Ecology Interactions among species and their environment occur over the organisms' entire lifetimes. Most marine animals have larval stages (see Fig. 15.11), and seaweeds have spores. What happens to the larvae and spores can be more important than interactions later in life.

Many factors can affect how many larvae survive. Some larvae are sensitive to changes in temperature, salinity, and other factors, so larval survival may vary depending on oceanographic conditions. Larvae may also have a critical period during which they must obtain the right food to survive. The survival of haddock larvae off the coast of Nova Scotia, for example, is closely linked to the availability of the plankton that they eat during a few critical weeks in the early spring. In years when weather and oceanographic conditions favor an abundance of plankton during this period, the larvae survive particularly well and there are more adults of these fish in later years. Predators, pollution, and many other factors can also have a strong influence on larval survival.

If the larvae do survive they still must reach the habitat where they will live as adults. Some larvae remain near their parents, but the drifting larvae of many marine species depend on favorable currents to carry them to the right place. It has long been assumed that currents scatter most larvae far and wide, but it has recently been discovered that the larvae of at least some species are able to stay fairly close to the habitats where their parents produced them, making it easier for them to get back. The larvae of some coral reef fishes, for example, are surprisingly strong swimmers and are able to stay near their home reef, recognizing the reef by sound or perhaps smell. The larvae of other species tend to stay in water layers where there isn't much current, so they aren't carried far. If larvae do reach the right habitat, they have to recognize it and settle in the right place. The larvae of many bottom-dwelling species test the bottom before they settle. Others are attracted to chemicals produced by their hosts or adults of their own species (see Fig. 13.5).

In many marine communities it is unclear, and often controversial, whether the abundance of organisms is determined primarily by the supply of larvae to settle in the habitat (this school of thought has been dubbed "supply-side ecology") or by competition, predation, and other interactions after the larvae settle (see "Competition," p. 214). As with many controversies in marine ecology, the answer may well lie in the middle.

MAJOR MARINE LIFESTYLES AND ENVIRONMENTS

It has already been noted that, because physical and chemical conditions change from place to place, different parts of the ocean harbor very distinct communities. Marine biologists therefore categorize communities according to where and how the organisms live. Perhaps the simplest classification relates to the lifestyle of the organism: whether it lives on the bottom or up in the water column. **Benthic organisms,** or the **benthos,** are those that live on or buried in the bottom (Fig. 10.11). Some benthic organisms are **sessile,** or attached to one place; others move around. **Pelagic** organisms, on the other hand, live up in the water column, away from the bottom.

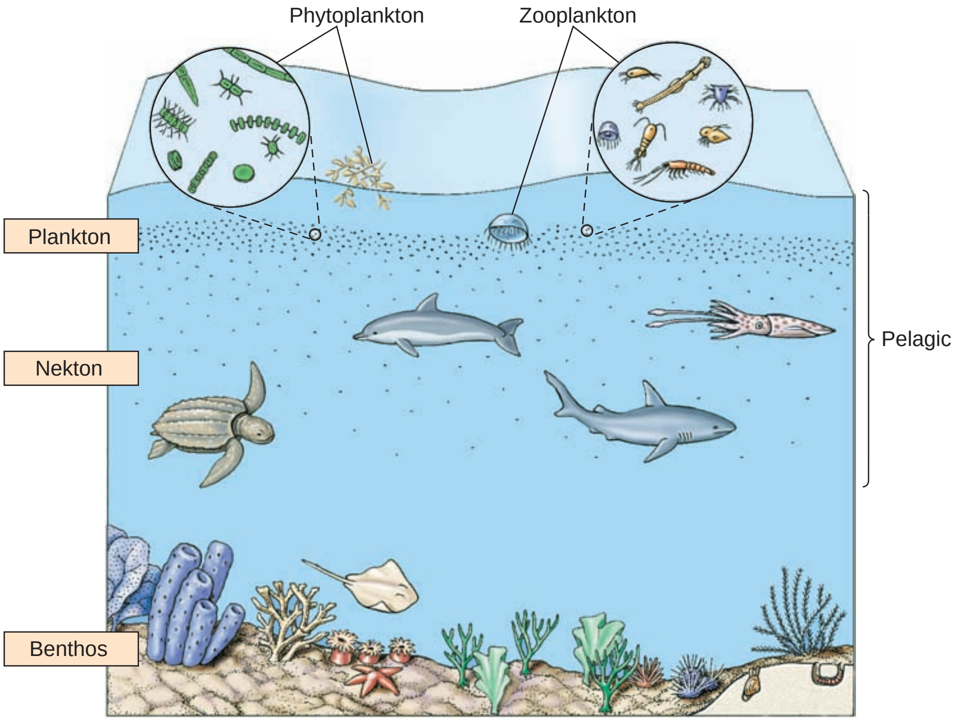


FIGURE 10.11 Three major groups, the benthos, nekton, and plankton, result when marine organisms are classified by lifestyle.

Pelagic organisms are further subdivided according to how well they can swim. Some marine organisms swim only weakly or not at all. These organisms, called **plankton,** are at the mercy of the currents and are carried from place to place. The term "plankton" comes from the Greek word for "drifters." Planktonic algae and other autotrophs are collectively called the **phytoplankton** and are the most important primary producers in many marine ecosystems. The heterotrophic plankton are called the **zooplankton.** The plankton can also be subdivided according to size, whether they live right at the sea surface or further below, or whether they spend all or only part of their lives in the plankton (see "The Organisms of the Epipelagic," p. 329, and "The Floaters," p. 339).

Animals that can swim well enough to oppose the currents are called **nekton.** Most nektonic animals are vertebrates, mainly fishes and marine mammals. There are a few nektonic invertebrates, however, such as squids. Not all nekton are pelagic. The ray in Figure 10.11, for example, is part of the nekton because it can swim. It is not considered pelagic, however, because it spends most of its time on or just above the bottom rather than up in the water column.

Another way to classify marine communities is by where they live. Zonation in benthic organisms, for example, relates to depth and the continental shelf (Fig. 10.12). Right at the boundary between land and sea is the shallowest part of the shelf, the **intertidal zone,** sometimes called the **littoral zone.** This is the area between the tides that is exposed to the air when the tide is out but underwater at high tide. The intertidal zone makes up only a small fraction of the continental shelf. Most of the shelf is never exposed to the air, even at the lowest of low tides. Benthic organisms that inhabit the continental shelf below the intertidal live in the **subtidal zone,** sometimes called the **sublittoral zone.** Away from the shelf the benthic environment is subdivided by depth into the **bathyal, abyssal,** and **hadal** zones. For the sake of simplicity, we shall lump these different zones together and call them the "deep-sea floor."

The pelagic environment, too, is divided with reference to the continental shelf. The pelagic environment that lies over the shelf is called the **neritic zone.** Pelagic waters beyond the **shelf break** are the **oceanic zone.**

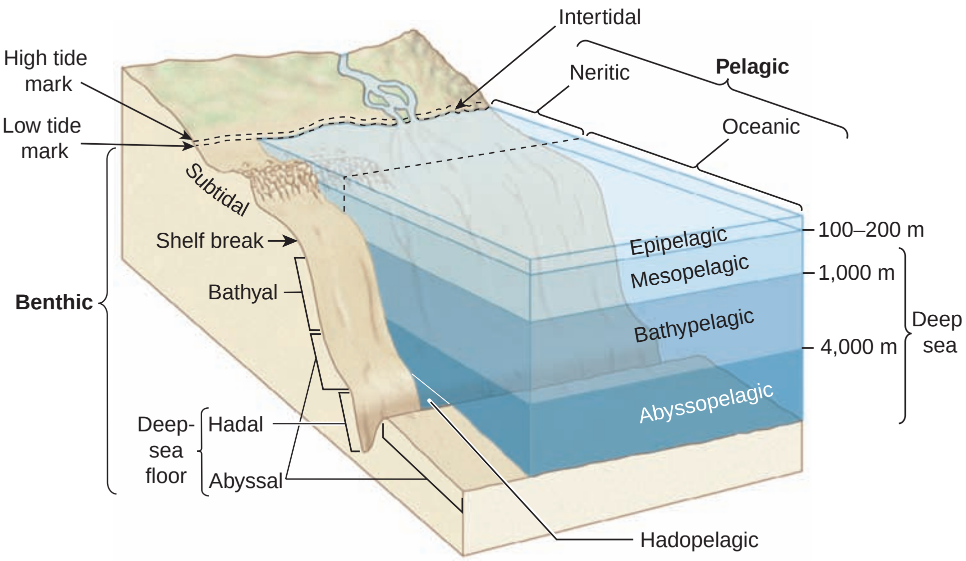


FIGURE 10.12 The major subdivisions of the marine environment are based on distance from land, water depth, and whether the organisms are benthic or pelagic.

Besides being divided into the neritic and oceanic zones, the pelagic is divided vertically into depth zones that correspond to the amount of light. In the shallowest, the **epipelagic zone,** there is plenty of light for photosynthesis, at least for part of the year. Given a supply of nutrients, phytoplankton thrive, producing food for the rest of the ecosystem. The epipelagic usually extends down to a depth of 100 to 200 m (350 to 650 ft). Because this is approximately the depth of the continental shelf, nearly all neritic waters lie in the epipelagic.

Other pelagic zones lie in the deep oceanic waters beyond the shelf. Below the epipelagic lies the **mesopelagic zone.** There is not enough light in the mesopelagic to support photosynthesis, so primary producers cannot grow. There is, however, enough light to see by. On even the brightest day, the mesopelagic is an area of twilight. This twilight zone typically extends to a depth of around 1,000 m (3,300 ft).

No sunlight at all penetrates to the deepest parts of the ocean, the **bathypelagic, abyssopelagic,** and **hadopelagic** zones. Although each of these zones supports a different community of animals, they share many similarities. We refer to all these zones together as the "deep-sea" environment.

THE FLOW OF ENERGY AND MATERIALS

All living things use energy to make and maintain the complex chemicals necessary for life. **Autotrophs** get this energy from the non-living environment, usually in the form of sunlight. They use the energy to make their own food from simple molecules like carbon dioxide, water, and nutrients. As the autotrophs grow and reproduce they become food for **heterotrophs** (Fig. 10.13). When one organism eats another, both the organic material and the energy stored in it are passed from one to the other. Thus, energy and chemical substances flow from the non-living part of the ecosystem to organisms and from organism to organism. The pathways taken by energy and materials tell us a lot about how an ecosystem works.

Trophic Structure

The flow of energy and matter through an ecosystem can be traced by observing the trophic relationships among its organisms: who makes the food and who eats it. The organisms can be divided into two broad components: **primary producers,** the autotrophs that make the food, and **consumers,** the heterotrophs that eat it. Not all consumers feed directly on producers. Many animals eat other consumers rather than primary producers. Thus, the transfer of energy through the system usually takes place in several steps known as a **food chain.** Each of the steps in the food chain is known as a **trophic level.**

Most ecosystems have a number of different primary producers. Furthermore, many animals eat more than just one kind of food, and many change their diet as they get older

Shelf Break The increase in steepness that marks the outer edge of the continental shelf.

- Chapter 2, p. 34

Autotrophs Organisms that can use energy (usually solar energy) to make organic matter.

Heterotrophs Organisms that cannot make their own food and must eat the organic matter produced by autotrophs.

- Chapter 4, p. 67

Primary Production The conversion of carbon dioxide into organic matter by autotrophs, that is, the production of food.

- Chapter 4, p. 68

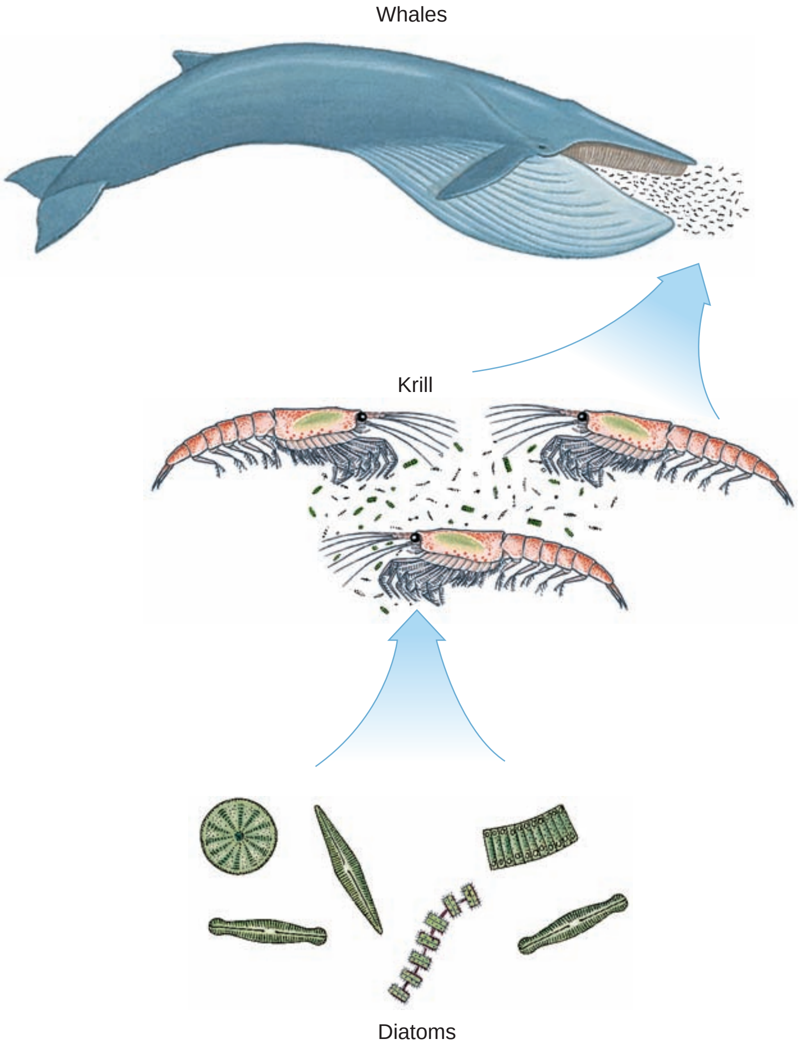


FIGURE 10.13 This three-step food chain is typical of Antarctic waters. Diatoms are primary producers that capture sunlight to fix carbon. Planktonic diatoms are the main primary producers during summer, but in winter diatoms and other algae growing in sea ice are more important. The energy is transferred from the diatoms to the krill that eat them, and then to blue whales that eat the krill. Though only part of a complex food web (see Fig. 10.14), this simple food chain accounted for a great deal of the total productivity of Antarctic waters until whales were hunted nearly to extinction.

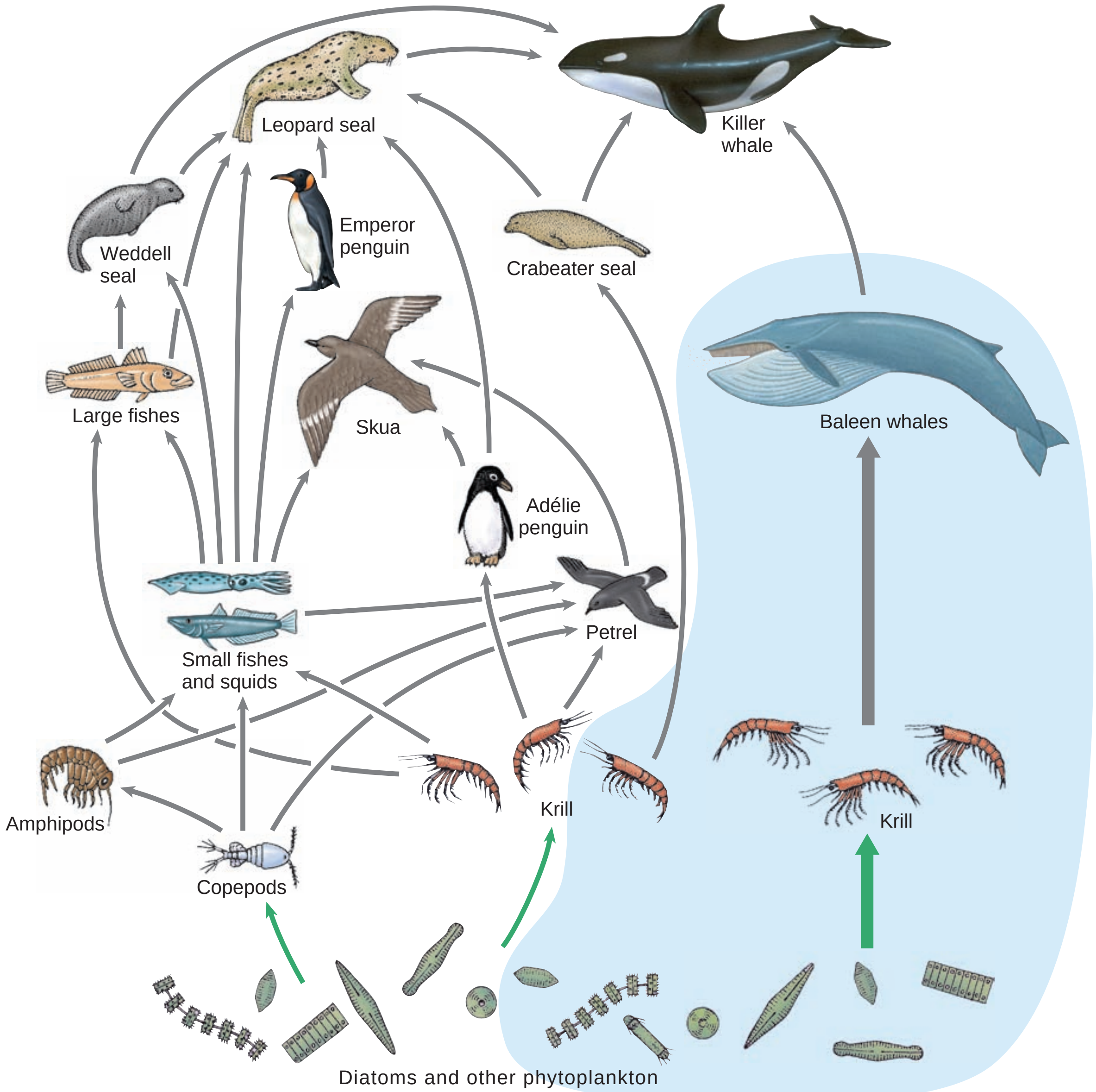

Killer whale
Leopard seal
Weddell seal
Emperor penguin
Crabeater seal
Large fishes
Skua
Baleen whales
Adélie penguin
Petrel
Small fishes and squids
Amphipods
Krill
Krill
Copepods
Diatoms and other phytoplankton

FIGURE 10.14 A simplified Antarctic food web. The simple diatom-krill-whale chain illustrated in Figure 10.13 (blue shading) is an important part of this food web.

and larger (see Fig. 15.24). For these reasons, trophic structure is usually a complex, interwoven **food web** (Fig. 10.14) instead of a simple, straight-line food chain. Such food webs are difficult for biologists to unravel and understand, but their complexity is one reason for the tremendous diversity of life.

Energy and materials are passed from one trophic level to another along a food chain or food web. The first level is occupied by primary producers, the other levels by consumers.

Trophic Levels Food chains and food webs are a little easier to understand if we consider the number of steps, or trophic levels, through which the energy passes (Fig. 10.15). The first step in the flow of energy, and therefore the first trophic level, is occupied by the primary producers that originally capture the energy and store it in organic compounds. Diatoms are the main primary producers in the food web illustrated in Figures 10.14 and 10.15. Consumers that feed directly on the producers are called **first-level,** or **primary, consumers** and occupy the next trophic level. At the level above that are **second-level,** or **secondary, consumers,** predators that eat the primary consumers. Feeding on the secondary consumers are the **third-level,** or **tertiary, consumers,** and so on. Each trophic level relies on the level below for sustenance. At the end of the food web are **top predators** such as killer whales.

The concept of trophic levels helps us understand how energy flows through ecosystems, but the organisms themselves are not concerned about which level they feed at. Predators often feed on prey from different trophic levels, for example.

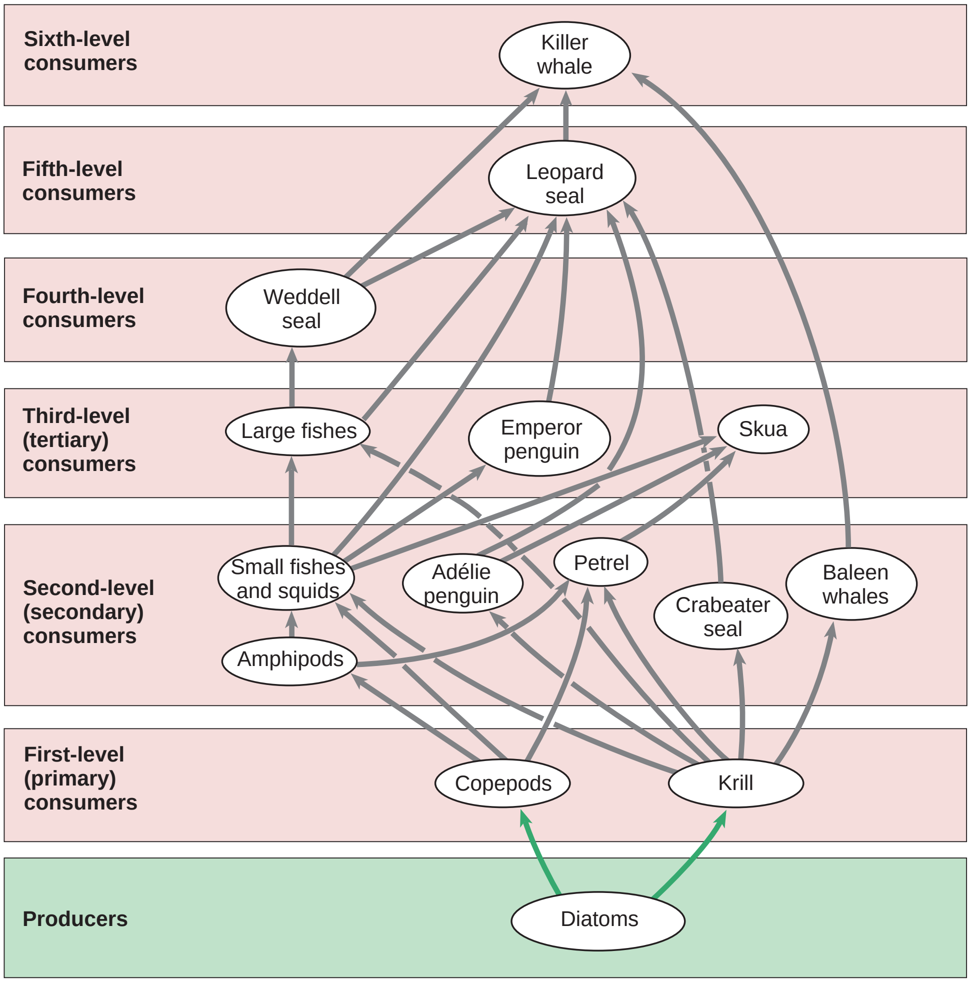


FIGURE 10.15 The organisms in the food web in Figure 10.14 can be grouped into categories according to their trophic level. The same organism, however, may feed at different levels. Petrels, for example, act as second-level consumers when they eat copepods but as third-level consumers when they eat amphipods. In this simplified diagram they are shown as second-level consumers. The food web shown here is longer than most; three or four levels are more common.

The Trophic Pyramid Instead of being passed on to the next higher level, much of the energy contained in a particular trophic level is used up by the activities of the organisms. Energy and organic matter are also lost as waste. Depending on the ecosystem, only about 5% to 20% of the energy in one trophic level is passed on to the next; an average is about 10%. Suppose, for example, that the diatoms in the Antarctic food chain illustrated in Figure 10.13 contain a total of 10 million calories of energy. According to the 10% rule, only about 1 million calories will make it to the primary consumers, the krill, and the whales will get only about 100,000 calories. The trophic structure of ecosystems can be represented by a **pyramid of energy** (Fig. 10.16), with less energy contained in each succeeding level.

Because there is less energy available at each level, there are also fewer individual organisms. Thus, there are fewer primary consumers than producers, and fewer secondary than primary consumers. Often, though not always, the **trophic pyramid** can be pictured in terms of numbers of individuals as well as energy and is then called the **pyramid of numbers** (see "Standing Stock," p. 224). The pyramid can also be expressed in terms of the total weight of tissue, or **biomass,** produced by the organisms at each level. In this case, the trophic pyramid is called the **pyramid of biomass.** To support a given biomass of primary consumers, primary producers must make about 10 times as much living tissue. To support 1,000 grams of copepods, for example, the copepods need to eat about 10,000 grams of phytoplankton. In turn, only about one-tenth of the primary consumer's biomass will make it to the secondary consumers.

On the average, only about 10% of the energy and organic matter in one trophic level is passed to the next higher level.

At each step in the food web some organic matter is lost rather than being eaten by higher-level consumers. This material is not lost to the ecosystem, however. Decay bacteria, fungi, and other **decomposers** break down this non-living organic matter into its original components: carbon dioxide, water, and nutrients. Some of the organic matter is excreted as waste, is spilled during feeding, or leaks out of cells by diffusion. This material dissolves in the water, so it is known as **dissolved organic matter (DOM).** There is also a lot of dead organic matter in solid form, such as decaying seaweeds, cast-off seagrass and mangrove leaves, discarded exoskeletons, pellets of feces, and dead bodies. This material is called **detritus.** Detritus is an important energy pathway in marine ecosystems because many marine organisms feed on it. Large populations of microscopic decomposers live in association with detritus, and detritus feeders often derive as much or more nutrition from the decomposers as from the detritus itself. Similarly, many organisms eat the microorganisms that decompose DOM. Thus, decomposers play a vital role in the ocean by channeling dead organic matter back into the food web.

Waste organic matter that is dissolved in the water is called dissolved organic matter (DOM). Detritus consists of non-living, solid organic matter. Decomposers help channel DOM and detritus back into the food web.

If it were not for decomposers, waste products and dead bodies would accumulate instead of rotting away. Not only would this make quite a mess, but nutrients would remain locked up in the organic matter. When decomposers break down organic matter, the nutrients incorporated into the organic matter during primary production are released, making the nutrients available

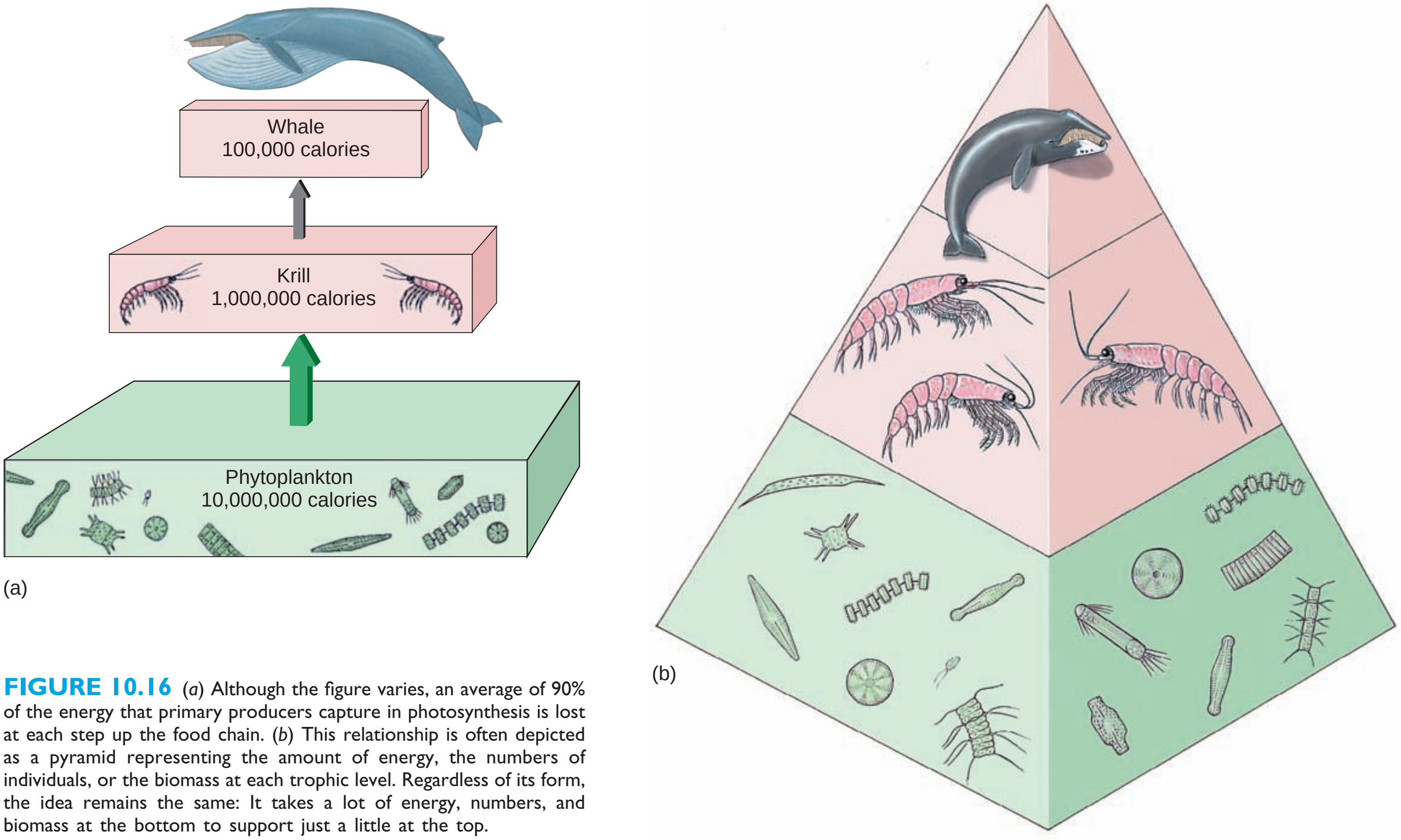


FIGURE 10.16 (*a*) Although the figure varies, an average of 90% of the energy that primary producers capture in photosynthesis is lost at each step up the food chain. (*b*) This relationship is often depicted as a pyramid representing the amount of energy, the numbers of individuals, or the biomass at each trophic level. Regardless of its form, the idea remains the same: It takes a lot of energy, numbers, and biomass at the bottom to support just a little at the top.

again to photosynthetic organisms. This process is known as **nutrient regeneration.** Without it, nutrients would not be recycled and made available to autotrophs, and primary production would be greatly reduced.

Measuring Primary Productivity Because primary production supplies the food at the base of the trophic pyramid, it is useful to know how much production occurs in a given area. The rate of primary production, or **productivity,** is often expressed as the amount of carbon fixed under a square meter of sea surface in a day or in a year (Fig. 10.17). It includes the production of both phytoplankton in the water column and producers that live on the bottom.

The total amount of organic carbon manufactured by primary producers is called the **gross primary production.** Primary producers immediately respire some of the organic matter they make to meet their own energy needs, however, so it is not available as food to other organisms. It is the organic matter that is left over, or the **net primary production,** that forms the base of the trophic pyramid.

Net primary production by **photosynthesis** can be estimated by measuring either the amount of raw material used up or the amount of end products given off by photosynthetic organisms in the sunlight. Traditionally this was done by measuring the amount of oxygen (O_2) produced (Fig. 10.18) but now it is more common to measure the amount of carbon dioxide (CO_2) consumed. This method uses an **isotope** of carbon (^{14}C) that can be measured very accurately. To measure gross primary production, **respiration** by the primary producers can be estimated by keeping them in the dark where no photosynthesis can occur. Other methods to estimate primary production include measuring the amount of light absorbed by the producers and measuring the glow, or fluorescence, that chlorophyll emits when it absorbs sunlight.

The rate of primary production is usually measured in light and dark bottles. Changes in the oxygen or carbon dioxide level in the light bottle indicate both photosynthesis and respiration, whereas changes in the dark bottle reflect only respiration.

In the ocean the amount of primary production varies dramatically from one environment to the other (Table 10.1). Some marine environments are as productive as any on earth. Others are biological deserts, with productivity as low as any desert on land. Productivity in the ocean depends largely on the physical characteristics of the environment, in particular on the amount of light and nutrients that are available. These characteristics will be explored in subsequent chapters.

Standing Stock The total amount of phytoplankton in the water, called the **standing stock** or **standing crop** of phytoplankton, is related to the primary productivity, but the two are not the same thing. The standing stock refers to how much phytoplankton

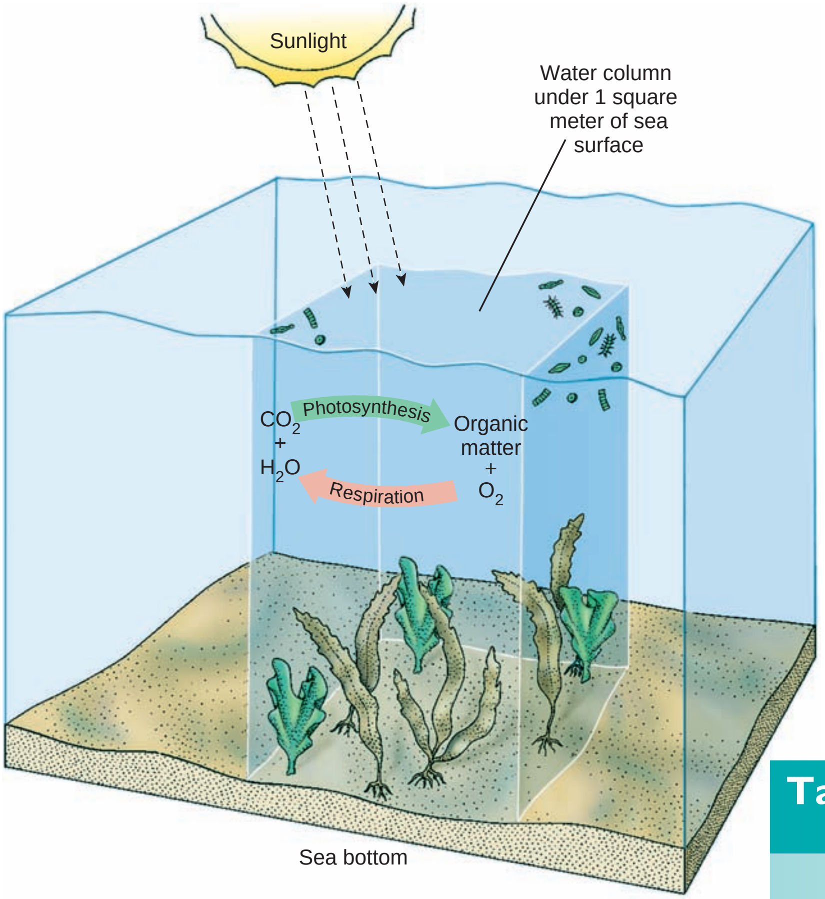


FIGURE 10.17 To describe primary productivity, marine biologists determine how much carbon ends up being fixed, or converted from carbon dioxide to organic material, in the water column under 1 m^2 of sea surface in a given time. Gross primary production refers to the total amount of organic matter produced; net primary production is the amount left over after the respiration of the primary producers themselves. Primary productivity is expressed in units of grams of carbon per square meter per day or year (gC/m^2/day or gC/m^2/year).

is already in the water. Primary productivity refers to the amount of new organic material being created. In a lawn, for example, the standing stock would correspond to the length of the grass. The primary productivity would be the amount of clippings produced if the lawn were mowed every day to keep it the same length.

This difference between primary productivity and standing stock explains why the trophic pyramid is not always reflected in a pyramid of numbers (see "The Trophic Pyramid," p. 223). A lawn that is growing very fast will produce a lot of clippings even if it is kept short. In other words, it can have high productivity but low standing stock. In the ocean, it often happens that when primary producers are growing very fast they are also eaten very fast. With lots of food available, the herbivore population grows, keeping the number of primary producers low. As a result, the pyramid of numbers is turned upside down, with more herbivores than primary producers. The pyramid of biomass refers to the productivity, not the standing stock, so like the pyramid of energy the pyramid of biomass always holds true.

Phytoplankton contain chlorophyll, so the amount of chlorophyll in the water is a good indication of phytoplankton abundance. Indeed, the most common way to measure the phytoplankton standing stock is to measure the concentration of chlorophyll in the water.

The standing stock of phytoplankton is the total amount of phytoplankton in the water column. Standing stock is usually determined by measuring the chlorophyll concentration.

Photosynthesis
$CO_2 + H_2O$ + sun energy → organic matter (glucose) + O_2
- Chapter 4, p. 66

Respiration
Organic matter (glucose) + O_2 → $CO_2 + H_2O$ + energy
- Chapter 4, p. 67

Isotopes Different atomic forms of an element.
- Chapter 2, p. 32

Table 10.1 Typical Rates of Primary Production in Various Marine Environments

Environment	Rate of Production (Grams of Carbon Fixed/m^2/yr)
PELAGIC ENVIRONMENTS	
Arctic Ocean	<1–100
Southern Ocean (Antarctica)	40–260
Subpolar seas	50–110
Temperate seas (oceanic)	70–180
Temperate seas (coastal)	110–220
Central ocean gyres*	4–40
Equatorial upwelling areas*	70–180
Coastal upwelling areas*	110–370
BENTHIC ENVIRONMENTS	
Salt marshes	250–2,000
Mangrove forests	370–450
Seagrass beds	550–1,100
Kelp beds	640–1,800
Coral reefs	1,500–3,700
TERRESTRIAL ENVIRONMENTS	
Extreme deserts	0–4
Temperate farmlands	550–700
Tropical rain forests	460–1,600

Note: Production rates can be much higher at certain times or in specific locations, especially at high latitudes. Values for some selected terrestrial environments are given for comparison.

*See "Patterns of Production," p. 346.

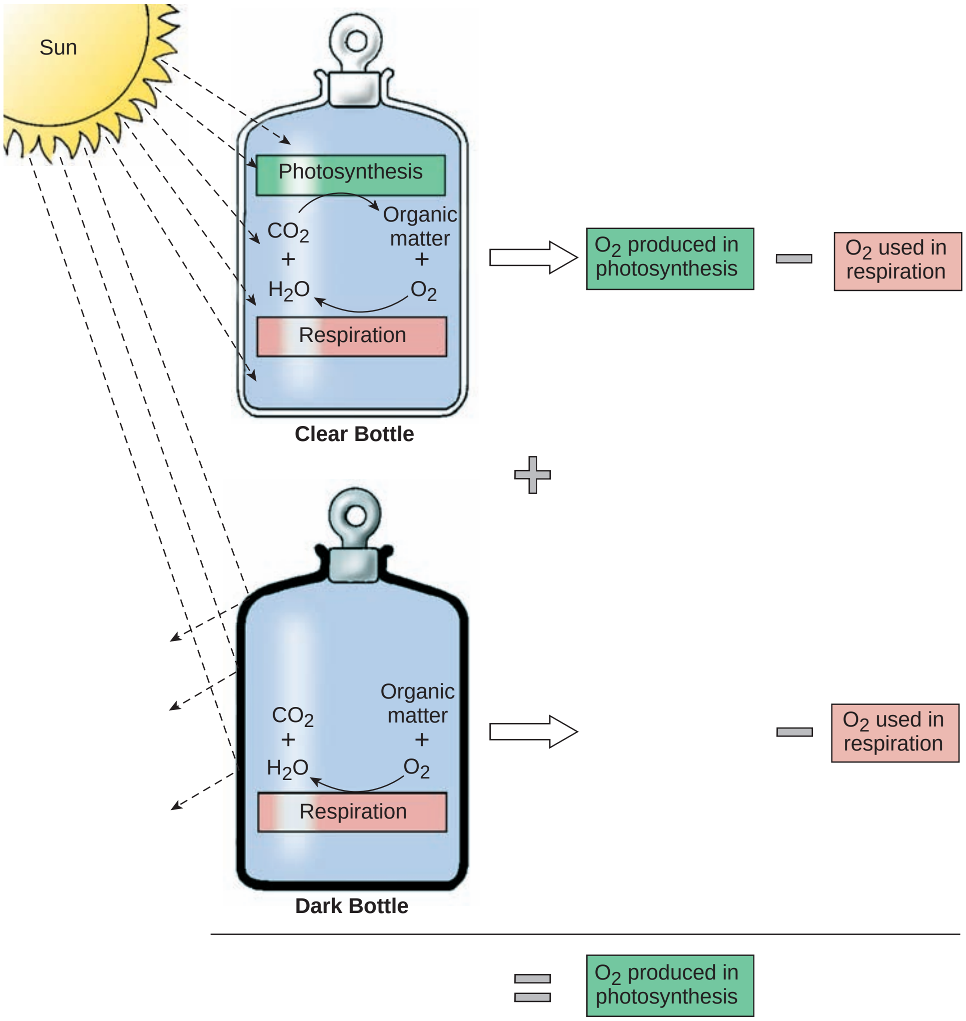


FIGURE 10.18 To measure primary production scientists put seawater samples in both clear and dark bottles. The clear bottle allows light to enter, so both photosynthesis and respiration take place. The amount of oxygen produced reflects the balance of photosynthesis over respiration, or the net primary production. To calculate the total production of organic matter by photosynthesis the amount of respiration must be known. This can be measured from the amount of oxygen used up in the dark bottle, where only respiration occurs because the light is blocked.

Chlorophyll can be measured by chemically extracting it from the water, but that is time-consuming and expensive. Instead, an instrument called a fluorometer is usually used to determine the amount of chlorophyll present from its fluorescence.

Phytoplankton standing stock can also be measured from space. Satellites equipped with special cameras take color pictures of the sea surface and beam the images to earth. Using computers, scientists carefully analyze the photos, paying special attention to the characteristic green color of chlorophyll. Phytoplankton standing stock can be estimated over vast areas of the sea surface (Fig. 10.19) by applying various correction factors, taking account of the weather at the time the photo was taken, and relating the results to actual chlorophyll measurements made from ships. Satellites are the only means for assessing the large-scale distribution of phytoplankton; ships can measure standing stock at only one place at a time.

Cycles of Essential Nutrients

Once the energy stored in organic compounds is used in metabolism or given off as heat, it is lost to the system forever. Unlike energy, the *materials* that make up organic matter can be used over and over in a repeating cycle. These materials, like carbon, nitrogen, and phosphorus, originally come from the atmosphere, the earth's interior, or the weathering of rocks. Starting out as simple inorganic molecules, they are converted into other forms and incorporated into the tissues of autotrophs. When this organic material is broken down by digestion, respiration, and decomposition, the raw materials are released back to the environment, and the cycle begins again. Human alteration of these natural global cycles could have profound impacts on life on earth that we are not yet able to predict.

The **carbon cycle** provides a good example of this process (Fig. 10.20). The carbon that forms the backbone of all organic molecules starts in the atmosphere as carbon dioxide, then dissolves in the ocean. CO_2 is highly soluble in seawater, so the oceans holds more than 50 times as much carbon as the atmosphere. This inorganic carbon is converted into organic compounds by photosynthesis. Respiration by consumers, decomposers, and the producers themselves breaks down the organic compounds and makes the carbon dioxide available to producers again. Some carbon is also deposited as calcium carbonate in **biogenous sediments** and coral reefs. These contain 25 times again as much as the ocean. Under certain conditions, some of this calcium carbonate dissolves back into the water. Humans have greatly affected the global carbon cycle by burning fossil fuels and increasing the amount of CO_2 in the atmosphere (see "The Greenhouse: Too Much of a Good Thing?" p. 232).

Nitrogen, like carbon dioxide, is present in the atmosphere. Atmospheric nitrogen, however, is in the form of nitrogen gas (N_2), which most organisms are unable to use. Some cyanobacteria, other bacteria, and archaea can perform **nitrogen fixation,** and lightning also fixes atmospheric nitrogen. Without fixed nitrogen, algae and plants would not be able to get the nitrogen they need. In addition to nitrogen fixation that takes place in the ocean itself, fixed nitrogen enters the ocean from rivers and from the atmosphere in rain.

Human activities, however, now produce more fixed nitrogen than natural sources, and most of the fixed nitrogen entering the ocean comes from agricultural fertilizers (either directly or as animal and human waste), cultivation of nitrogen-fixing crops, and fossil fuel burning.

> Nitrogen fixation is the conversion of atmospheric nitrogen gas into a form that organisms can use. It is performed naturally by certain cyanobacteria, other bacteria, and archaea, but human activities now account for the majority of fixed nitrogen in the ocean.

Once nitrogen has been fixed, it cycles within the ecosystem as part of the **nitrogen cycle** (Fig. 10.21). There are several nutrient forms of nitrogen, the most important of which is **nitrate (NO_3^{-1}).** Nitrate and other nitrogen compounds are taken up during primary production and regenerated by decomposition. Most of the nitrogen-containing nutrients used in primary production come from this recycling of nitrogen compounds, not the original fixation of nitrogen. Until recent times natural nitrogen fixation was balanced by **denitrification,** which converts fixed nitrogen back to N_2, so the amount of fixed nitrogen in the global environment was more or less constant. Natural denitrification is no longer able to keep up with human activities, however, and fixed nitrogen is building up with potentially catastrophic consequences (see “Overwhelming the Nitrogen Cycle,” p. 236).

Most of the phosphorus entering the ocean is brought in by rivers in the form of **phosphate (PO_4^{-3}),** although a small amount is deposited from the atmosphere. Much of this phosphate is derived naturally

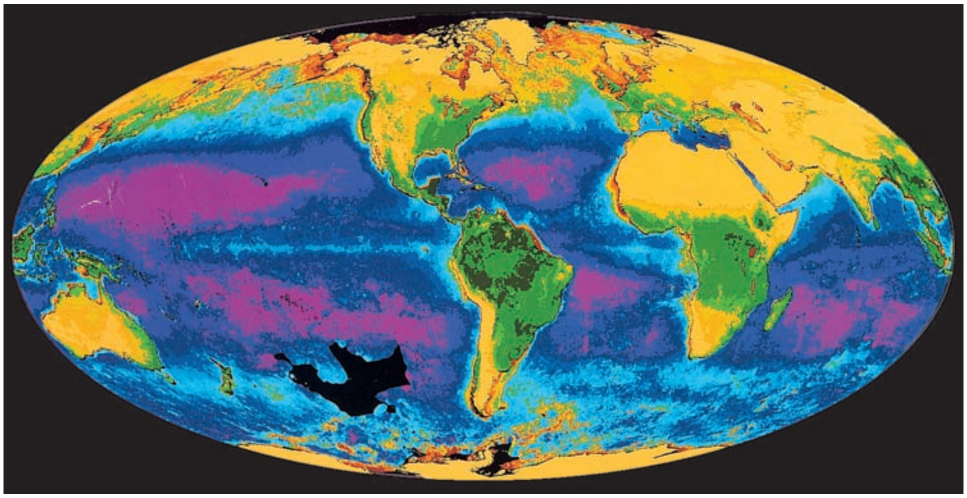


FIGURE 10.19 A global view of the distribution of primary producers on earth. The parts of the ocean with the highest amounts of phytoplankton pigment are shown in red and yellow; dark blue and violet represent areas with the lowest phytoplankton concentration. Note that phytoplankton are scarce over much of the ocean’s surface. On land, desert and ice areas are shown in yellow, while the most productive forests are in dark green.

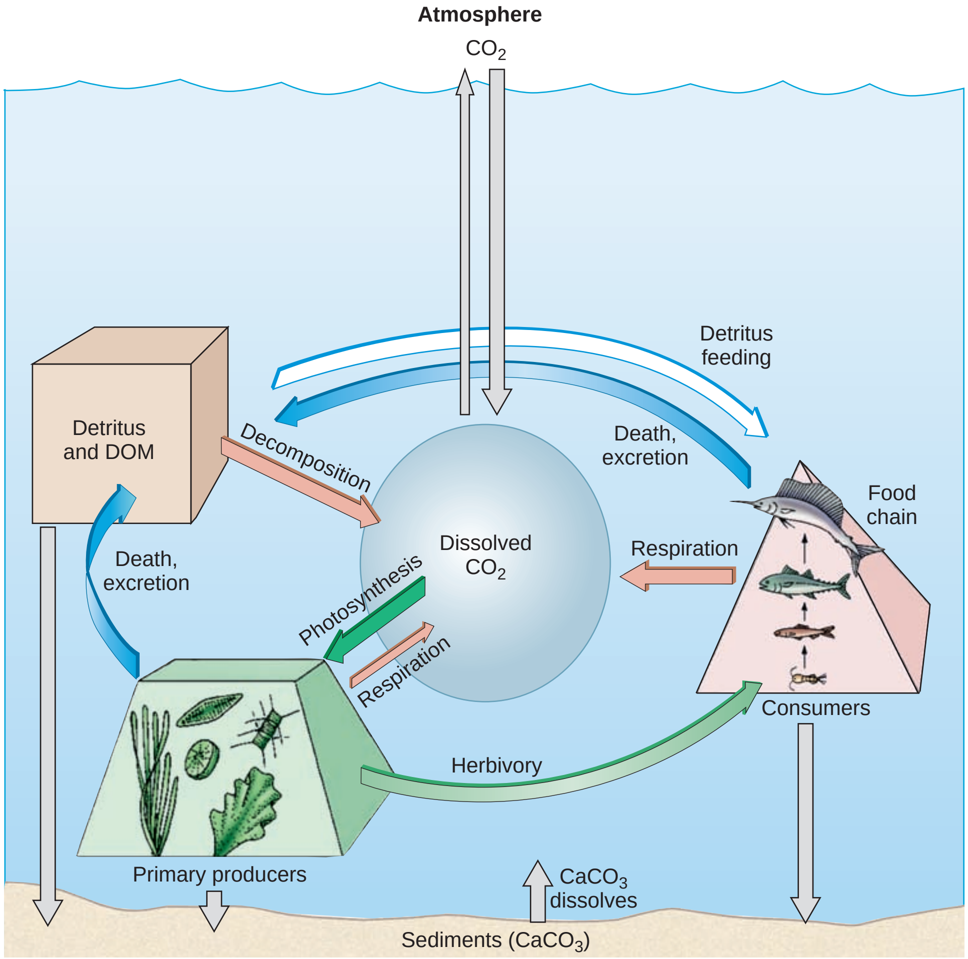


FIGURE 10.20 The carbon cycle in the ocean. Carbon dioxide (CO_2) from the atmosphere dissolves in the ocean. In photosynthesis, primary producers convert carbon dioxide into organic matter, which is then passed to animals and other consumers in the food chain. Both producers and consumers release carbon dioxide as a product of their respiration. The rest of the carbon fixed by autotrophs eventually is excreted as waste or ends up in the form of dead bodies. This non-living organic matter forms detritus and dissolved organic matter (DOM). Bacteria and other decomposers break down this organic matter, releasing carbon dioxide and starting the cycle anew.

Biogenous Sediment Made of the skeletons and shells of marine organisms.
Weathering The physical or chemical breakdown of rocks.
- Chapter 2, p. 32

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.
- Chapter 5, p. 93; Table 5.1

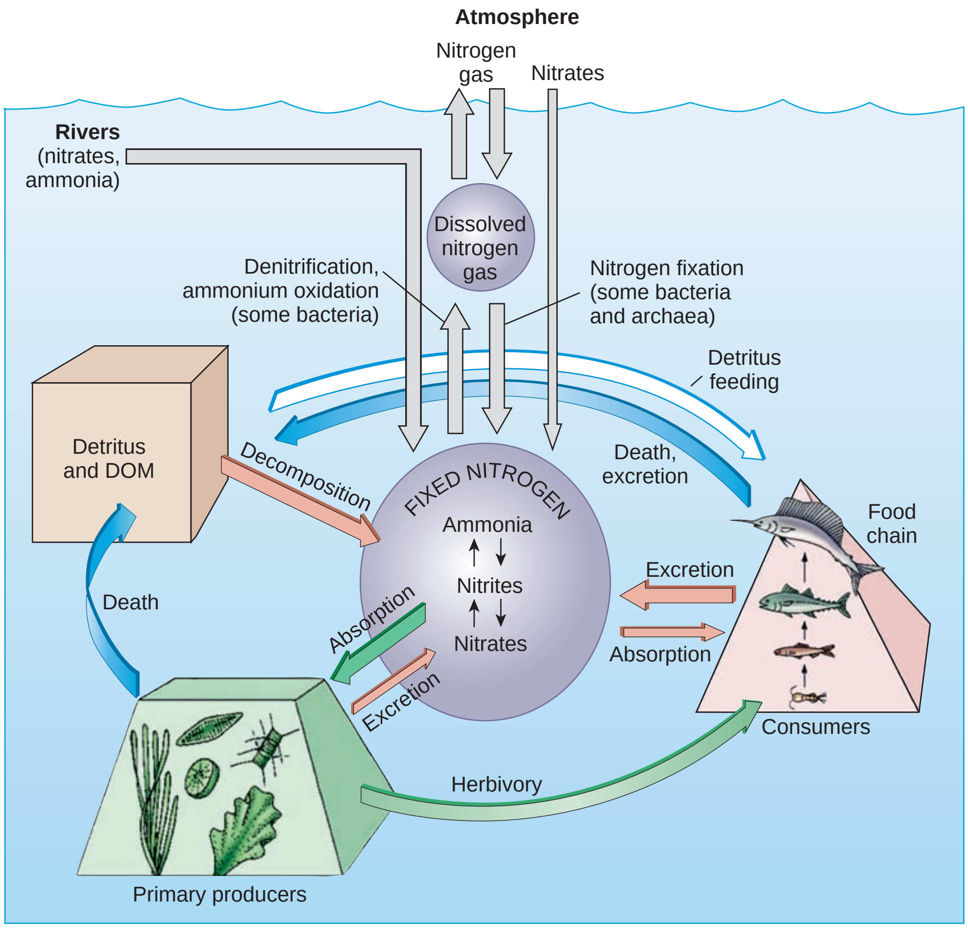

Atmosphere
Nitrogen gas
Nitrates
Rivers (nitrates, ammonia)
Dissolved nitrogen gas
Denitrification, ammonium oxidation (some bacteria)
Nitrogen fixation (some bacteria and archaea)
Detritus feeding
Detritus and DOM
Decomposition
FIXED NITROGEN
Ammonia
Nitrites
Nitrates
Death, excretion
Food chain
Excretion
Absorption
Death
Absorption
Excretion
Consumers
Herbivory
Primary producers

FIGURE 10.21 The nitrogen cycle in the ocean. The atmosphere is rich in nitrogen gas (N_2), which cannot be used by most organisms. Some cyanobacteria, other bacteria, and archaea convert N_2 into a usable form of nitrogen by the process of nitrogen fixation. There are several different forms of usable nitrogen; various bacteria and archaea convert nitrogen from one usable form to another (see Table 5.1). Primary producers take up the usable nitrogen to produce organic matter. The nitrogen is then passed on to animals and other consumers when they eat the organic matter. Usable nitrogen may be excreted as waste by producers and consumers or regenerated by decomposing bacteria.

from the **weathering** of rocks and bird guano on land, but a great deal comes from fertilizers and other human sources as well. On the other hand, humans sometimes reduce phosphate input to the ocean because phosphate gets trapped in sediment that builds up behind dams. After primary producers take up the phosphate and incorporate it into organic matter, the phosphorus cycles in organic form through the food web (Fig. 10.22). Phosphorus is deposited in ocean sediments either in biogenous sediments or through **chemical precipitation,** in which chemical reactions convert phosphate into insoluble forms that settle on the sea floor. Some phosphorus is transported from the ocean back to land by seabirds and deposited as guano (see “Of Fish and Seabirds, Fishers and Chickens,” p. 389) but the flow of phospho-

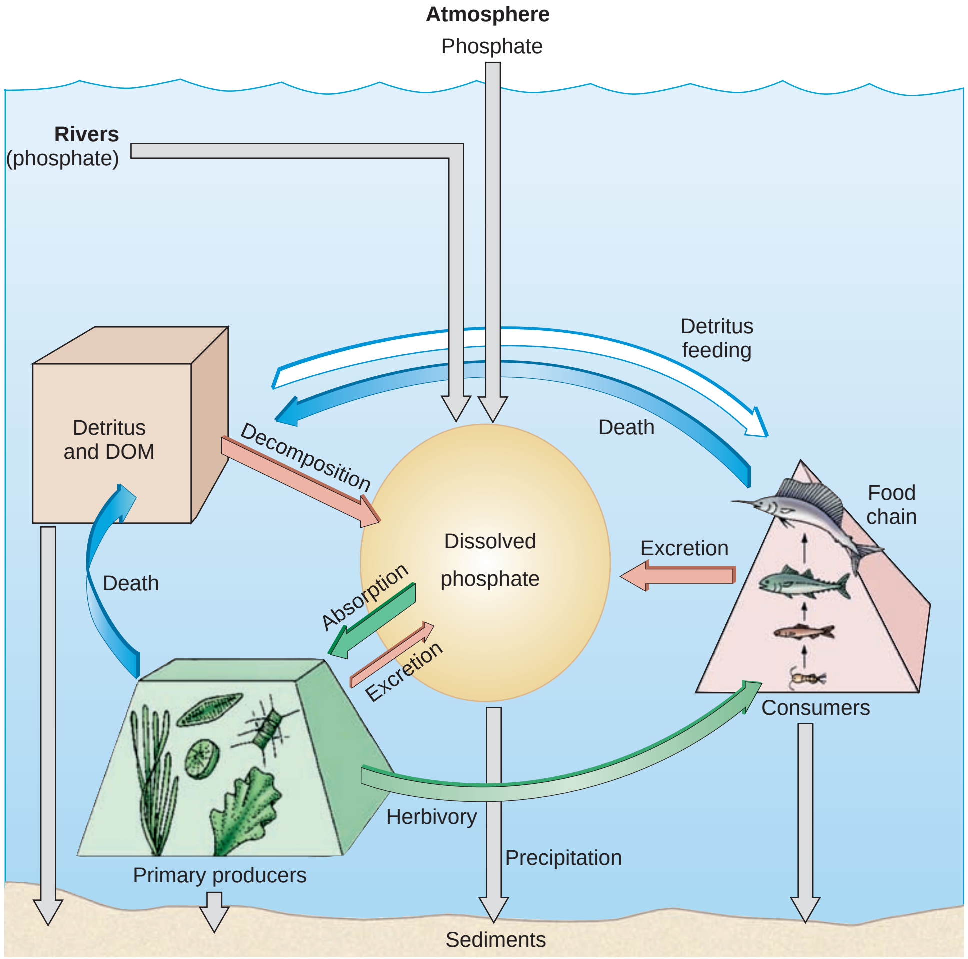

Atmosphere
Phosphate
Rivers
(phosphate)
Detritus feeding
Detritus and DOM
Decomposition
Death
Dissolved phosphate
Food chain
Excretion
Death
Absorption
Excretion
Consumers
Herbivory
Precipitation
Primary producers
Sediments

FIGURE 10.22 The phosphorus cycle in the ocean. Most phosphorus enters the ocean as phosphate in rivers. Primary producers incorporate the phosphate into organic matter, which is passed on up the food chain or becomes detritus or dissolved organic matter. The phosphorus in organisms and detritus is deposited in biogenic sediments. Dissolved phosphate is also deposited when chemical reactions convert it into insoluble forms that precipitate to the sediments.

rus through the ocean to the sediments is mostly a one-way street. Over millions of years, however, the phosphorus is recycled by geological processes such as the uplift of marine sediments onto land.

Other raw materials needed by organisms, like silicon and iron, undergo similar cycles. The tremendous abundance and diversity of living things depend on this recycling. Without it, the living world would soon run out of raw materials, and life on earth would be scarce indeed.

The living world depends on the recycling of materials such as carbon, nitrogen, and phosphorus. Decomposition is a vital part of this cycle.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Two species of sea urchins live practically side by side on sandy bottoms. The two species appear to have the same diet: drift seaweeds and other bits of organic matter. They are able to live in the same environment without competing with each other. How might they be able to share their habitat and food resources?
2. It is not always easy to categorize a particular case of symbiosis. Suppose a certain species of snail is always found living on a certain coral. No one has found evidence that the snail harms the coral, so the relationship is classified as an example of commensalism. How would you go about testing this hypothesis? What kinds of observations might lead to the conclusion that the snail is a parasite, or that it has a mutualistic relationship with the coral?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

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SPECIAL REPORT: Our Changing Planet

Our planet never stops changing, in cycles that range from the hundreds of millions of years over which continents drift apart and reform to the annual change of seasons and even the daily cycle of night and day. These cycles are Earth's natural rhythms, but humans are changing our planet in ways and at rates unprecedented not just in recorded history but on geological timescales. Where once we weren't aware of our impacts on "spaceship Earth," we now know that some of our activities are changing the entire planet. It could be that everything will be all right—anything is possible. By continuing these activities unabated, however, humanity has embarked on a vast global experiment, gambling that the fundamental processes that provide our most basic needs—air, food, water, and shelter—will stand up to whatever we do.

Rolling the Dice: Climate Change

The earth is getting warmer. Global temperatures have steadily increased over the last 150 years (Fig. 1), rising by about 0.6°C (1.1°F) during the 20th century. As of 2006, the six warmest years on record occurred during the previous decade, the three warmest were since 1998, and 19 of the 20 warmest occurred since 1980. We already know, however, that climate goes through regular cycles, not just over the tens or hundreds of thousands of years it takes for ice ages to come and go, but also over centuries. Viking and other histories recount a "Medieval Warm Period" from about AD 850–1250, overlapping a period of high solar activity. That was followed by the "Little Ice Age," a time of bitterly cold weather in Europe from roughly 1500 to 1850. It could be, then, that the 20th-century rise in temperature is just another natural fluctuation.

It is important to understand the difference between climate and weather. "Climate" means average conditions over decades or longer, whereas "weather" refers to short-term conditions over days or months. Cold weather in Miami—a frost, say—doesn't mean Miami has a cold climate. A snap of cold weather for a few weeks, or even an unusually cold winter, doesn't tell us anything about how climate might be changing, nor is one heat wave proof of global warming. To judge the 20th-century temperature rise we need to know how climate has fluctuated in the past.

Reliable, widespread measurements with thermometers go back only to about 1850, but there are natural temperature records of past climates, including ocean sediments (see "The Record in the Sediments," p. 32), corals, ice cores (Fig. 2), tree rings, pollen, boreholes in continental rock, and historical records such as the extent of Arctic sea ice or how far north grapes could be grown. One such reconstruction, called the "hockey stick" graph (Fig. 3),

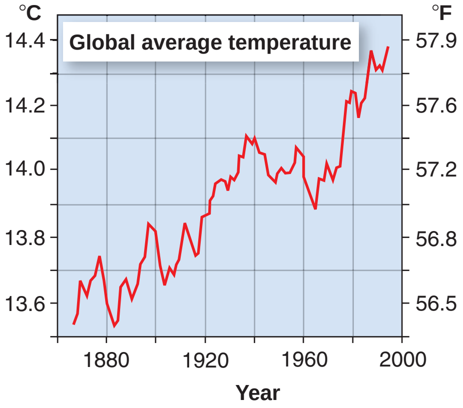


Figure 1 Global average temperature, 1886–1994.

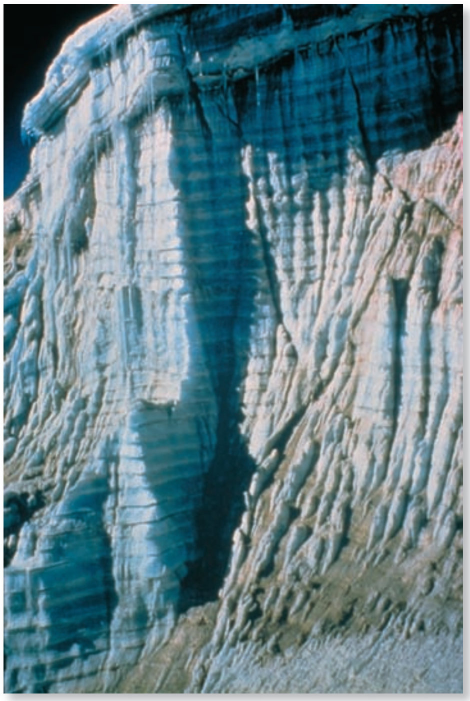


Figure 2 Annual bands of ice, like these from Perú's Quelccaya ice cap in the Andes, are one way scientists can tell what past climates were like.

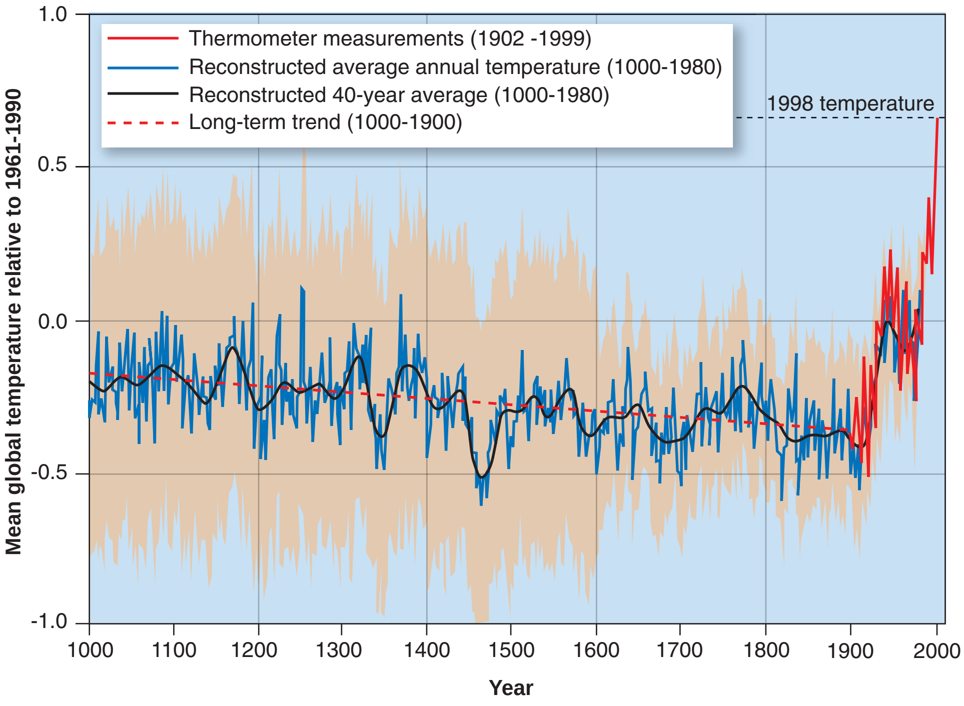


Figure 3 Recent thermometer measurements and past temperatures estimated from tree rings, ice cores, corals, and historical records. The light brown shading indicates the range of uncertainty. Even with this uncertainty, 1998 was the warmest year in a millenium.

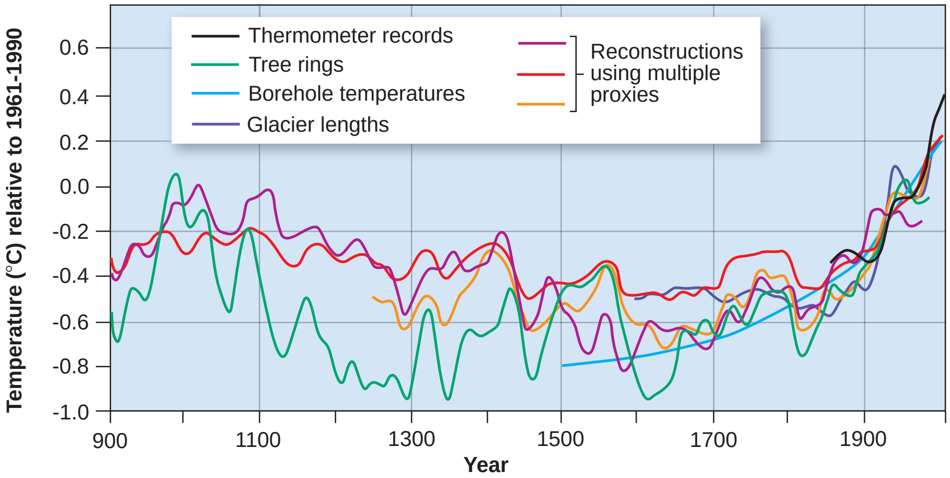


Figure 4 Subsequent studies have confirmed the rapid 20th-century warming shown in Figure 3. The reconstructions using multiple proxies are independent analyses of different sets of data from tree rings, glaciers, boreholes, sediments, chemical composition of ice cores and fossils, and other natural temperature records.

shows a small, steady cooling from the 9th to the 19th centuries (the "handle"), followed by a rapid temperature rise in the 20th century (the "blade"). The hockey stick graph was vehemently attacked by skeptics, many with ties to the fossil fuel industry, but later studies using new, independent information have repeatedly confirmed the sharp warming in the 20th century to temperatures not seen in at least four centuries and probably a millennium or more (Fig. 4). The Medieval Warm Period and Little Ice Age are almost insignificant by comparison. The warming is not evenly distributed: The Arctic and Antarctica are warming faster than the rest of the globe.

Sea temperatures change more slowly than the atmosphere, but the ocean is also warming (Fig. 5). An estimated 84% of the total heating of the planet between 1955 and 2003 went into warming the ocean—otherwise we would be experiencing much hotter temperatures.

The overwhelming evidence has led a group of hundreds of the world's top scientists known as the International Panel on Climate Change (IPCC), the United States National Research Council, and virtually every major scientific study this century to conclude that global climate change is real. A large majority of scientists have also concluded that human activities are the cause, by intensifying a natural phenomenon known as the **greenhouse effect.**

The Greenhouse: Too Much of a Good Thing?

Our climate is controlled by light energy from the sun. Some is reflected back into space, but most is absorbed by the planet's atmosphere and surface (including the ocean) and converted from light to heat. Like the glass of a greenhouse, trace amounts of **greenhouse gases** in the atmosphere are transparent to light energy but block heat transmission back to space. The heat is retained and warms the earth (Fig. 6). Without this greenhouse effect the earth's surface would average about −19°C (2°F), some 33°C (59°F) colder than it is, and would be inhospitable to life as we know it.

The most important greenhouse gases are ordinary water vapor, carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (NO_2). Water vapor isn't a very potent greenhouse gas, but the atmosphere has so much that it accounts for most of the greenhouse effect. But atmospheric water is a product, not the cause, of the greenhouse effect. If other greenhouse gases didn't warm the earth in the first place, all the water would be locked up in ice. And given a greenhouse effect, the amount of atmospheric water vapor is purely a function of temperature: Any water added, whether naturally or through human activities, simply falls back out as precipitation within days. Thus, although water vapor amplifies the

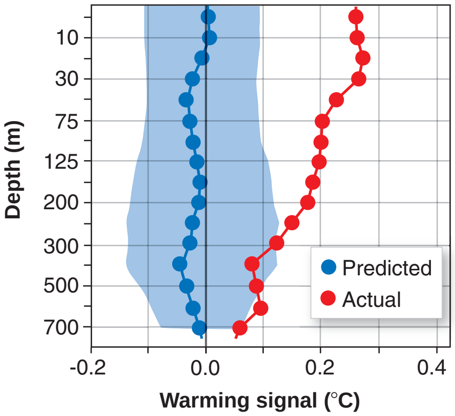


Figure 5 Ocean warming. If the North Atlantic hasn't warmed or cooled since there should be no temperature change (or "warming signal") at any depth, represented here as vertical line at 0.0 °C. The shaded area shows the range of natural variation. Model predictions that include only natural factors like solar and volcanic activity (blue) show that natural drivers alone would be expected to result in a slight cooling at some depths. Actual temperature measurements (red), however, show a significant warming to a depth of more than 700 m (2,300 ft). Other ocean basins show a similar trend.

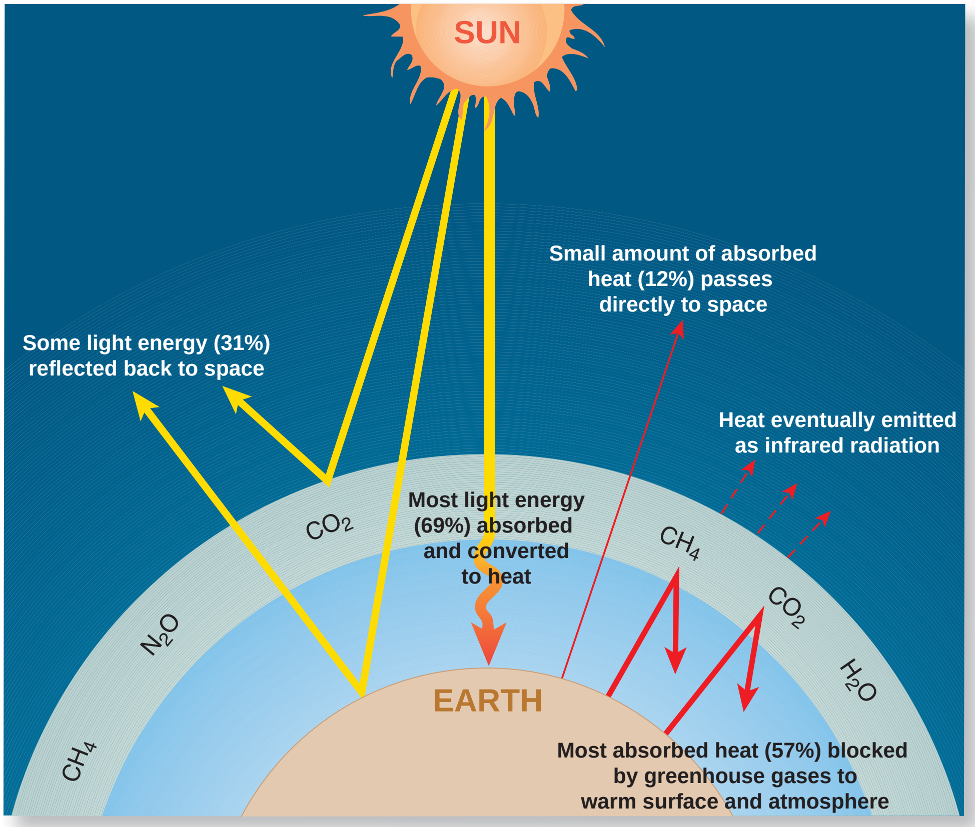

SUN
Small amount of absorbed heat (12%) passes directly to space
Some light energy (31%) reflected back to space
Heat eventually emitted as infrared radiation
Most light energy (69%) absorbed and converted to heat
CO_2
N_2O
CH_4
CH_4
CO_2
H_2O
EARTH
Most absorbed heat (57%) blocked by greenhouse gases to warm surface and atmosphere

Figure 6 The green house effect.

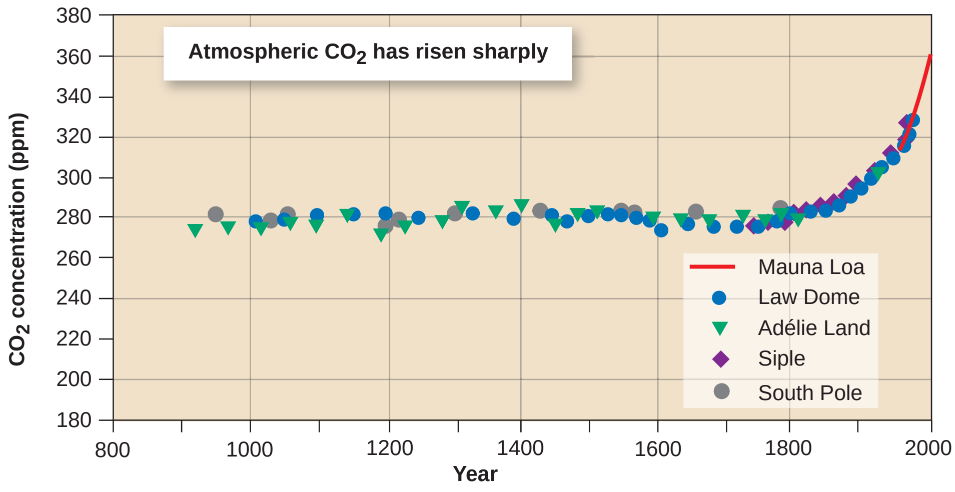


Figure 7 Atmospheric CO_2 levels over the last millennium, estimated from several sources.

greenhouse effect, it is the other greenhouse gases that actually drive it. The most important of these is CO_2.

CO_2: Through the Roof

In the natural carbon cycle, atmospheric CO_2 levels are controlled primarily by air-sea exchange and biological activity (see Fig. 10.20). Tiny bubbles of air trapped in polar ice record greenhouse gas levels at the time the ice formed. The temperature at the time can be determined from isotope ratios in the ice itself. Antarctic ice cores show that over multiple ice ages atmospheric CO_2 levels fluctuated between only about 180 and 280 parts per million (ppm, equivalent to 0.018–.028%). Variability in the other major greenhouse gases has been similarly constrained. These fluctuations in greenhouse gases are not enough to produce glacial cycles, which are driven primarily by fluctuations in the earth's orbit and axis of rotation that affect the amount of solar energy striking the planet. Volcanic activity has a minor impact, mainly by injecting aerosols, microscopic particles, into the upper atmosphere, where they increase the reflection of sunlight and slightly cool the earth. Thus, in pre-industrial times extending back through at least eight major ice ages, greenhouse gases fluctuated in concert with other natural cycles.

Since about 1750, and particularly since the expansion of the industrial revolution in the mid-19th century, human activity has disrupted these cycles. Atmospheric CO_2 levels have gone through the roof (Fig. 7). CO_2 has increased at about 1.5 ppm per year since measurements on Mauna Loa, Hawai'i, began in 1958 (Fig. 8). The CO_2 concentration is now 380 ppm, 35% higher than any time prior to 1750 in at least the last 800,000 years. The rate of increase is more than 200 times faster, which is more important because the parts of the carbon cycle that remove CO_2 from the atmosphere—dissolution in the ocean, photosynthesis, and deposition in sediments—cannot keep up. Other greenhouse gases have also risen dramatically: Atmospheric methane, for example, has more than doubled. The effect of all greenhouse gases together is now equivalent to about 430 ppm CO_2.

The increase in atmospheric CO_2 is a direct result of human activities: In recent decades about three-quarters of the increase is a result of burning coal, oil, and other fossil fuels and most of the rest has come from intensified land use, particularly the burning of forests and other biomass. This is not disputed by even the most hardened skeptics. The main human sources of methane are fossil fuels, the digestive systems of cattle and sheep, rice paddies, and landfills. Only the human-induced increase in greenhouse gases can account for the rapid warming observed over the last several decades (Fig. 9).

What's Happening Now?

Some consequences of global warming are already apparent. Sea level is rising because of the expansion of surface waters as they warm and the melting of glaciers and icecaps. This has been happening since the end of the last ice age, but the rate is accelerating: Sea level rise has averaged 1.5 mm/yr (0.06 in/yr) since 1870, 1.8 mm/yr (0.07 in/yr) from 1961 to 2003, and 3.1 mm/yr (0.12 in/yr) between 1993 and 2003. Particularly worrying is the recent discovery that the great ice sheets covering Greenland and Antarctica are losing ice to the oceans despite the fact that warming has also produced snowfall increases in some places. Scientists didn't expect the ice sheets to start melting until next century. Apparently the sheets don't just melt from the top, as was thought. Instead, melt water trickles down cracks in the ice to lubricate ice flow over the underlying rock, so that the entire ice sheet flows to the sea faster. Antarctic sea-ice shelves are shrinking, or even collapsing and drifting away as icebergs, as did large parts of the Larsen B Ice Shelf on the Antarctic Peninsula in 2002. This doesn't immediately affect sea level because the ice is already floating. But, the ice shelves act as dams to slow the flow of glaciers on land, and when the ice shelves are gone the glaciers move to the ocean faster. Arctic sea ice is also shrinking to record lows. The loss of sea ice also has ecological consequences (see below). Climate change–driven shifts in ocean circulation, rainfall patterns, and storm frequency may also have already occurred.

Global warming is also changing the biosphere. Many species on land—by some estimates more than half, at least in temperate areas—have been affected. Plants are flowering, birds are migrating, butterflies are

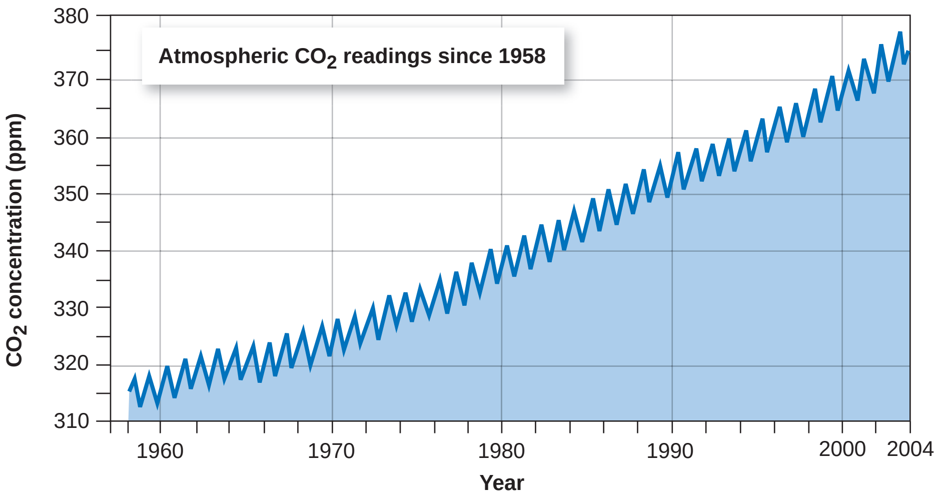


Figure 8 Atmospheric CO_2 measurements from Mauna Loa, Hawai'i.

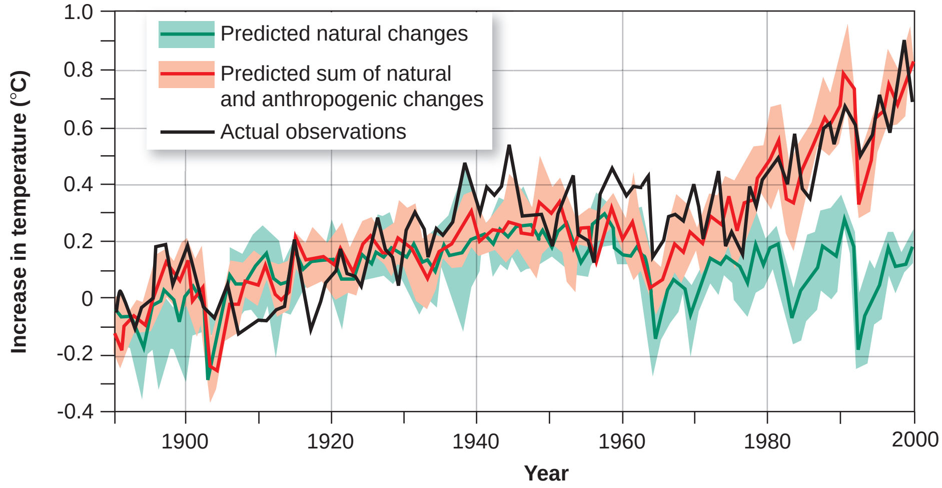


Figure 9 Models that consider only solar and volcanic activity but leave out the effects of greenhouse gas increases (green, line shows average and shading shows variability) indicate that global temperatures should have remained stable over the last century. The model results only match actual temperature observations (black line) if the effects of greenhouse gases are included (red).

appearing, and frogs are breeding earlier in the year, for example, as the warm days of spring arrive sooner.

Marine organisms have also been affected. Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*) have steadily moved closer to the South Pole, following the disappearing sea ice on which they depend, while open-water-feeding chinstrap *(P. antarctica)* and gentoo *(P. papua)* penguins have followed in their wake into the newly ice-free waters. Krill have declined in large parts of the Antarctic, as the sea-ice algae they depend on to get through the winter have disappeared along with the ice; this could affect the entire food web. Declining sea ice is also altering marine ecology in the Arctic. Polar bears (*Ursus maritimus*), for example, are in decline because the receding ice limits their ability to venture from land to hunt. In late 2006 the United States Fish and Wildlife Service proposed to list polar bears as threatened, the first time a United States government agency acknowledged climate change as a threat to any species.

Climate-driven changes in marine ecosystems are not limited to polar regions. There is a growing consensus among biologists that climate change is a threat to coral reefs: Mass coral bleaching and mortality in response to locally high surface temperatures are becoming more frequent, more intense, and widespread. In temperate regions the distributions of many intertidal, plankton, and fish species have shifted toward the poles along with their preferred temperature ranges and other climate-related factors. Two-thirds of North Sea fish species moved either northward or deeper between 1977 and 2001, and the northern limit of the blue mussel *(Mytilus edulis)* in Norway moved north by more than 1,000 km (600 mi) to the Svalbard Islands in the Arctic where the mussel had not been recorded for 1,000 years. Phytoplankton communities in the California Current system have shifted toward warmer-water species (Fig. 10). Similar changes are occurring all over the world.

Climate change may already be affecting entire food webs as well as species distributions. The recruitment of larval cod *("Gadus" morhua)* in the North Sea, for example, may have declined because warm-water species of zooplankton are less suitable food for young cod than the cold-water species they are replacing. There may also be mismatches in life history. Reproduction of many zooplankton species is timed to coincide with the spring bloom of phytoplankton. Whereas the phytoplankton bloom is triggered by increased day length and light availability, temperature is the reproductive cue for many zooplankton. Warmer temperatures are occurring earlier in the spring, but day length and light levels are unchanged. Zooplankton may therefore be reproducing before the peak in their phytoplankton food, with effects that could move up the rest of the food web.

What Lies Ahead?

The earth system takes time to balance out, and even if humanity immediately ceased all greenhouse gas emissions the earth would warm by another 0.5–1.0°C (0.9–1.8°F) above today's temperatures over the next several decades. This is a "warming commitment" we have already made that cannot be reversed. But of course we won't—we can't—simply stop all our greenhouse gas emissions tomorrow. Even stabilizing greenhouse gases at today's levels would require drastic cuts of 70–80% in emissions from current levels within a few decades—that is already out of reach. Without effective steps to reduce emissions, CO_2 levels are expected to increase to 490–640 ppm by 2050 and 620–1250 ppm by the end of the century; on our current path (Fig. 11) the levels will be at the high end of this range. These increases correspond to global average temperatures 1.7–6.4°C (3.1–11.5°F) warmer than in the period 1980–1999. Feedbacks in the system could make our planet warm even more, or faster, than these projections (see "Will There Be a Last Straw" p. 236). As temperature rises, so will sea level, by a conservatively estimated 18–59 cm (7–23 in) by 2100. Much depends upon the great ice sheets in Antarctica and Greenland: If they begin melting irreversibly, sea level would rise by as much as 12 m (39 ft). Current projections are that this would take several centuries to perhaps a millennium, but recent observations that ice sheets are melting much faster than expected have scientists rethinking their predictions.

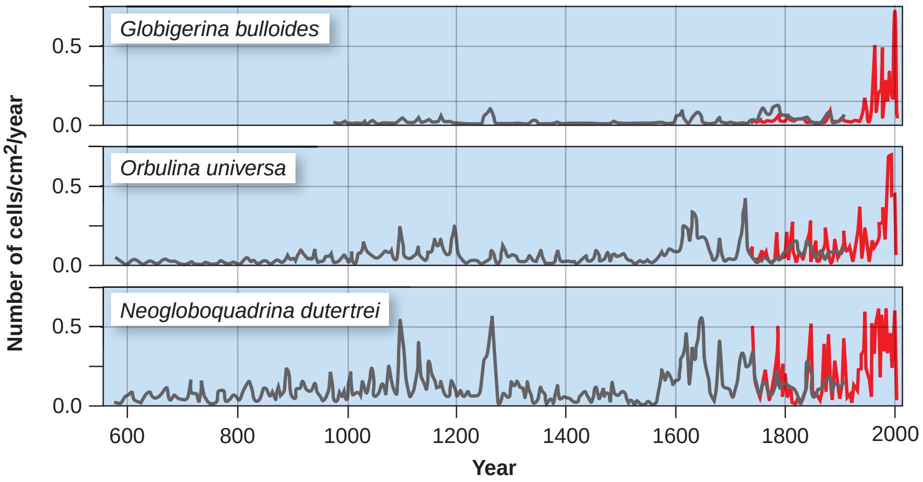


Figure 10 Abundance of three warm-water planktonic foraminiferan in sediment cores from the Santa Barbara basin extending back 300 and 1400 years (red and black lines, respectively; *G. bulloides* was not counted in the earliest samples). These species were occasionally abundant in the past, but their sustained abundance during the twentieth century marks a significant change to warmer conditions.

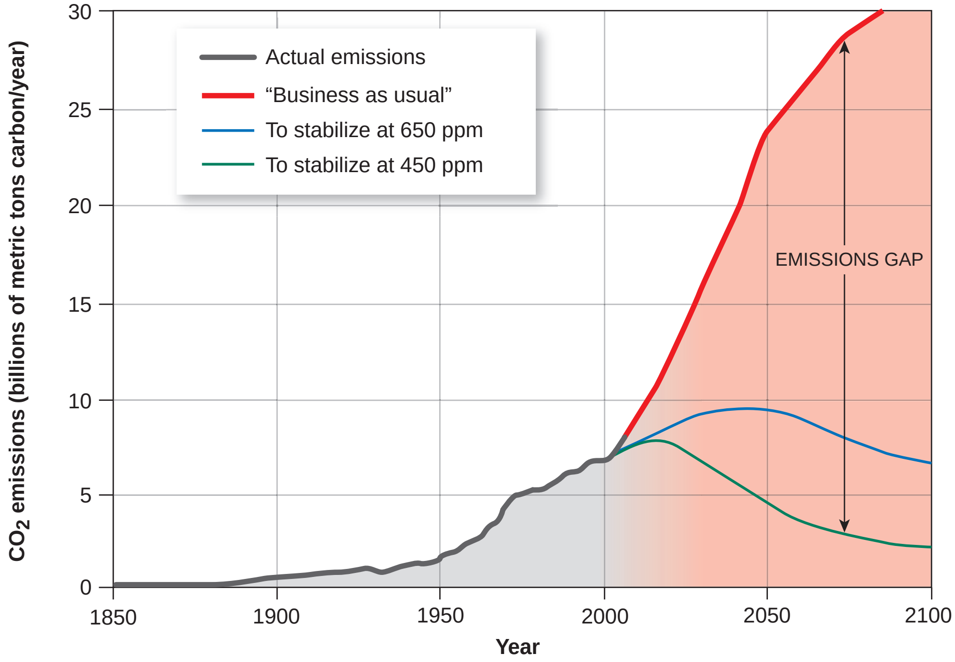


Figure 11 So far, global CO_2 emissions are following a path predicted by a fossil-fuel-intensive, business-as-usual model, which by 2100 would produce CO_2 levels of 750–1250 ppm and rising. This can be compared with emissions pathways we need to be on to stabilize atmospheric CO_2 concentrations at 450 or 650 ppm.

So What?

Temperatures a few degrees warmer might not sound like much, but even a 3°C (5.4°F) temperature rise will make the earth its warmest in 3 million years, far beyond the 10,000-year experience of human civilization. One of the main effects will be to speed up the water cycle. The higher temperatures will promote evaporation, and rainfall will increase globally. The increase will not, however, be evenly distributed. Climate change is expected to intensify existing patterns so that places that are wet now will experience more frequent and more severe floods, while drought and forest fires become worse in arid regions. People who depend on melting snow and glaciers for their summer water supplies, for example in the western United States, western Europe, and western China, will suffer increasing late-summer water shortages as the snow season shortens, as melting takes place earlier in the year, and as glaciers shrink and disappear. Globally, an estimated 1 to 4 billion people face increasing water shortage. Although increased atmospheric CO_2 may have a slight "fertilizing" effect on some crops, overall agricultural yields are expected to decline, mostly in developing countries. Fisheries, already faced with drastic overfishing, could be further threatened if the changes in marine ecosystems that are already occurring continue and intensify. Hundreds of millions more people will be at risk of hunger and malnutrition.

Sea level rise will increasingly threaten coastal areas, home to more than 40% of the world's population and most of its largest cities, including New York, Los Angeles, London, Shanghai, Cairo, and Rio de Janiero. This won't be a case of cities washed away overnight in a Hollywood-style inundation. Instead, coastal erosion will gradually increase, requiring ever more expensive seawalls and other protective measures, or the gradual abandonment of buildings, refineries, dockyards, and other shoreline infrastructure. Saltwater incursion will cause increasing problems with stormwater drainage, water supply, and sewage systems. Just as importantly, coastal areas will become more vulnerable to storms, floods, and other extreme events—not just because of the rising seas but also because storms and floods are expected to become more frequent, more extreme, and possibly more widespread. There is evidence, though still controversial, that this has already occurred. Increasing coastal vulnerability combined with more extreme weather could well mean more disasters like Hurricane Katrina (see "Sand on the Run, or What to do With our Shrinking Beaches," p. 418).

Human health will also suffer. Drought, floods, extreme storms, and malnutrition will inflict more and more casualties. Crippling heat waves will also claim more lives, though this will be partly offset by fewer deaths from extreme cold in northern climes. Damage to sanitation systems by floods, storms, and seawater incursion, and increasing shortages of safe drinking water, are expected to raise the toll from dysentery, cholera, and other intestinal diseases. As mosquitoes, ticks, and other hosts spread into areas that were once too cold for them they will spread diseases like malaria, West Nile fever, dengue fever, and encephalitis. The World Health Organization estimates that climate change during the 20th century is already killing 150,000 people a year, and another 1°C (1.8°F) increase will double that. We can't predict the health impacts of even greater warming, but they will probably increase well out of proportion to the temperature increase.

As to the cost, the most authoritative estimate to date is that the climate-change price tag for "business as usual" will be at least 5% of the entire global economy, each year, every year. When broader implications, like the risk of feedbacks (see "Will There Be a Last Straw" p. 236), come into play, the bill could rise to 20%. That would mean everybody on the planet gets 20% less goods and services, on average, than they would without anthropogenic climate change—in other words, a 20% "climate tax" paid by everyone, that can't be reduced by legislation. The predicted economic impact of climate change has been likened to that of the World Wars and Great Depression of the 20th century.

Ocean Acidification: The Other CO_2 Problem

Rising CO_2 levels will profoundly affect the ocean whether they change our climate or not. About half the CO_2 we pump into the atmosphere dissolves into the ocean. While that slows climate change from the greenhouse effect, it changes ocean chemistry. When CO_2 dissolves in seawater it forms carbonic acid, a weak acid also found in carbonated drinks. The resulting increase in acidity is measured as a lower pH. The ocean's acid balance is slightly on the alkaline side at around pH 8.0–8.3 (pure water is a neutral pH 7.0). The dissolved CO_2 increase from fossil fuel burning has already lowered the ocean's pH by about 0.1 pH units, and it could drop by 0.4 units by 2100 if CO_2 emissions continue to grow as they are now. These small changes in pH are more important than they might sound because the pH scale is logarithmic. A pH decline of 1 unit represents a 10-fold increase in the concentration of hydrogen ions (H^+)—what we measure as acidity—and a pH drop of only 0.1 means a 30% increase. The declining ocean pH is widely called **ocean acidification,** but the ocean is not expected to actually become acidic, only somewhat less alkaline. That doesn't mean there isn't a problem.

The organisms most at risk from ocean acidification are those that have shells, skeletons, or other structures made of calcium carbonate ($CaCO_3$). Lower pH makes calcium carbonate more soluble, increasing the tendency of carbonate structures to dissolve. The ocean's surface waters are supersaturated for calcium carbonate, so it doesn't dissolve there, but when the solubility balance is altered organisms make their shells slower and have to use more energy to do it. Lower pH also changes seawater's chemical balance to reduce the availability of the carbonate ions (CO_3^{-2}) needed to make calcium carbonate, again inhibiting calcification.

The CO_2 chemistry of seawater is well understood, and there is no doubt that ocean acidification is happening now and will intensify. The biological and ecological implications, however, are far less certain. Corals and certain groups of plankton, like pteropod molluscs (see Fig. 15.10), will probably be affected first because of the type of calcium carbonate they make. This could be the death knell for coral reefs, already stressed by warming-induced mass bleaching. Plankton communities could be radically altered, especially in the Southern Ocean where pteropods are an indicator of ecosystem health. As acidification becomes more severe it could damage other important plankton, like foraminiferans and coccolithophores, not to mention mussels, clams, snails, sea urchins, coralline algae, and a host of other organisms with carbonate structures. This might simply shift the ecological balance in favor of other species, with relatively little overall impact on ecosystems, or it could be catastrophic. Ocean acidification could enhance the growth of certain plankton that remove CO_2 from the atmosphere or produce gases that foster the formation of cooling clouds, but it might also cause a drop in the ocean's CO_2 uptake and further accelerate climate change. We know the oceans are acidifying, we just don't understand the consequences. We do know they are potentially huge—raising the stakes on our global roll of the dice.

Overwhelming the Nitrogen Cycle

Humanity is gambling with the nitrogen cycle as well as the carbon cycle. The earth has lots of nitrogen—more, in fact, than the other major essential elements (carbon, oxygen, phosphorus, and sulfur) put together. Nearly all of it, however, is in the form of dinitrogen gas (N_2). N_2 is practically inert and unavailable to organisms, so nitrogen is the element least available to life despite its abundance.

Before humans came along only lightning and a few microbes could convert N_2 into more reactive forms, including forms that primary producers can use as nutrients. The formation of these **reactive nitrogen** compounds was balanced by their conversion back to N_2 by microbes in the process of denitrification, limiting the pool of reactive nitrogen. Pre-industrial humans added to reactive nitrogen formation by cultivating legumes, rice, and other crops that boost the fixation of N_2 into nutrients the plants can use. By and large, denitrification was able to keep up with this increased formation of reactive nitrogen from agriculture.

Since the mid-1800s, however, human production of reactive nitrogen has increased 10-fold. The Industrial Revolution brought mass burning of fossil fuels, which converts nitrogen in the fuels as well as atmospheric N_2 to reactive nitrogen oxides (NOx). Cultivation of nitrogen-fixing crops

Will There Be a Last Straw?

We tend to expect that the climate system works like a thermostat: add some CO_2 and the temperature goes up, add a little more and the temperature goes up a little more. As long as the system behaves like that we can always hope that before things get too bad—next year, next decade, or next century—humanity can reduce its CO_2 emissions and things will cool down again. The planet probably doesn't work like that. There is increasing evidence of positive feedbacks in the climate system, whereby slight increases in temperature intensify the causes of warming, which intensifies the feedback effect, and so on. Some of these positive feedbacks are understood well enough to be included in current predictions, but others are "wild cards" in the global change game. There may be a "last straw" that breaks the camel's back of the global climate system. Here are some candidates—that we know about:

A Less Absorbent Sponge The ocean acts like a sponge for CO_2, absorbing about half our emissions. Because CO_2 is more soluble in colder water, warming seas will absorb less CO_2 and more will remain in the atmosphere.

Getting Steamed Water is the dominant greenhouse gas but it amplifies rather than drives greenhouse warming (see text). Higher temperatures mean more evaporation and more water in the atmosphere, creating a feedback loop. Recent measurements indicate a 6% increase in water vapor in the upper troposphere since 1982, pretty much as predicted by climate models.

Losing That Shine Almost a third of the solar energy striking earth is reflected back into space rather than being absorbed as heat (see Fig. 6)—creating "earthshine." Different aspects of global change are expected to affect Earth's reflectivity, or albedo, in different ways, but overall the albedo is expected to decrease, in particular as shiny white sea ice gives way to relatively dark, heat-absorbing open water in polar regions.

Clouding the Issue Higher moisture levels are likely to make the atmosphere more cloudy, especially if ocean acidification favors plankton that release cloud-promoting gases. Some scientists predict that the clouds will increase the earth's albedo, reflecting more heat into space to partially offset the greenhouse effect. Others argue that the greenhouse effect of the clouds themselves will be more important than the albedo change.

Disrupting the Conveyor The Great Ocean Conveyor circulation (see Fig. 3.25) that transports vast amounts of heat from tropical to polar regions is driven by temperature and salinity differences between surface and deeper water. Greatly increased freshwater input in the far north Atlantic, caused by melting Greenland ice, could shut down the conveyor circulation. Ironically that would bring much colder temperatures to Europe. Scientists have even speculated that it could trigger a "Little Ice Age" For Europe, but recent evidence indicates this is unlikely at least this century. Other regions, however, would warm even faster and the Asian monsoons could fail, bringing famine and hardship to millions.

Greenland Melting The accumulation of ice from high-elevation snowfall maintains Greenland's ice cap, replacing ice that melts at lower altitude. Once melting lowers the ice cap's elevation, snowfall will diminish and melting will accelerate because more of the ice cap will lie at lower, warmer altitudes. Only a new ice age could reverse this runaway process. The ice cap is 2 km (1.2 mi) thick, and if it melts entirely sea level would rise by about 7 m (23 ft). That would probably take a few thousand years, but in the meantime the flood of fresh water into the North Atlantic could shut down the conveyor circulation.

The Ocean Burps Ocean sediments hold more carbon, in the form of methane, than all the world's reserves of coal, oil, and natural gas. The methane, combined with water, is locked up in crystalline forms known as gas hydrates or clathrates. Warmer temperatures could destabilize the clathrates and suddenly release vast amounts of methane into the atmosphere. That would greatly intensify greenhouse warming, perhaps catastrophically.

Breaking the Soil Bank Soils are the second-largest of Earth's carbon reservoirs and absorb about a quarter of human CO_2 emissions. At the moment, soil absorption of CO_2 is increasing because higher atmospheric CO_2 levels stimulate plant growth. For now this helps slow greenhouse warming, but when temperatures rise high enough an increase in respiration by soil microbes and plants will overcome this effect and soils will release CO_2 instead of absorbing it. Furthermore, if peat bogs and wetlands dry out, and Arctic permafrost melts, they will release huge amounts of CO_2 and methane currently locked up in these soils.

also intensified: The amount of reactive nitrogen created by crops more than doubled between 1860 and 2000. Human creation of reactive nitrogen really took off after 1913 when the invention of the Haber-Bosch process, a method to convert N_2 into ammonia (NH_3), led to industrial-scale production of nitrogen fertilizers (Fig. 12).

Without these fertilizers global food production could never have kept up with our exploding population, and about 40% of today's population would go hungry. Poor soils and lack of access to fertilizer still mean hunger and malnutrition for people in some regions, and they need more reactive nitrogen, not less. But for the planet as a whole there is too much. Our production and use of reactive nitrogen is grossly inefficient. Creating reactive nitrogen by burning fossil fuels has no benefit at all, and only 12% of the nitrogen fertilizer applied to crops ends up in food. Most of the rest simply evaporates into the atmosphere or washes away into rivers, lakes, and the ocean.

As much as 70% of the reactive nitrogen in the environment now comes from human activities. Natural denitrification can't convert it back to N_2 fast enough, so reactive nitrogen is building up. The stuff is everywhere, flowing through the environment again and again in what has been called the **nitrogen cascade,** and overwhelming the natural nitrogen cycle. In the air, NOx compounds cause smog, leading to eye irritation, lung and heart disease, and cancer. Nitrous oxide (N_2O) is a greenhouse gas and contributes to the destruction of the ozone layer. Reactive nitrogen compounds in the atmosphere fall as acid rain, damaging lakes, rivers, and forests. In addition to acid rain damage, excess nitrogen falling onto forests, grassland, and other terrestrial systems causes a decline in primary productivity and the loss of biodiversity. Soil acidification also reduces agricultural production. Nitrates get into drinking water supplies, causing headache, fatigue, respiratory problems, and occasionally even death.

The nitrogen cascade is also harming the ocean. In many marine waters, phytoplankton and other primary producers are limited by a shortage of nitrogen nutrients like nitrate (NO_3^{-1}), and adding extra reactive nitrogen can produce excessive algal growth, or **eutrophication.** Many coral reefs, for example, are threatened by the overgrowth of seaweeds, caused at least in part by excessive nitrogen fertilization. Excess nitrogen input is also thought to be a major factor in a global increase in the extent and frequency of harmful algal blooms (Fig. 13), leading to ecosystem declines, lost fisheries revenue, and human health problems. Eutrophication is also linked to **hypoxic zones,** seasonal or

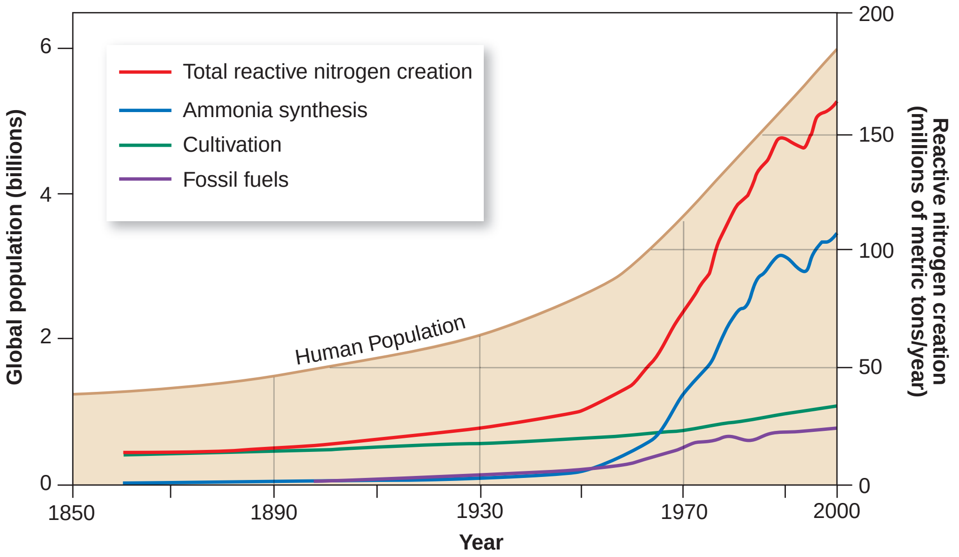


Figure 12 Reactive nitrogen creation by Haber-Bosch ammonia synthesis, the cultivation of nitrogen-fixing crops, and fossil fuel burning, 1860–2000.

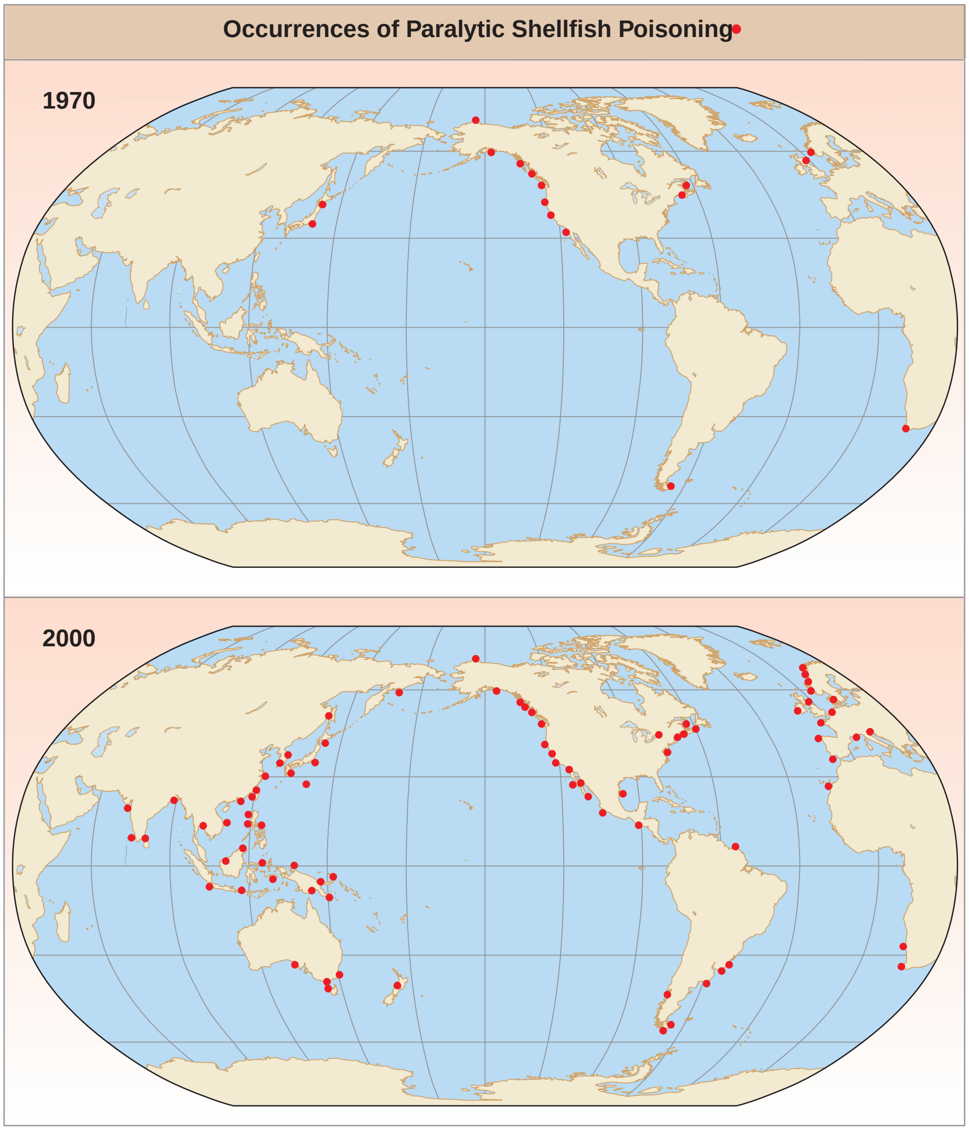


Figure 13 Increasing global occurrence of paralytic shellfish poisoning, one form of seafood poisoning caused by harmful algal blooms.

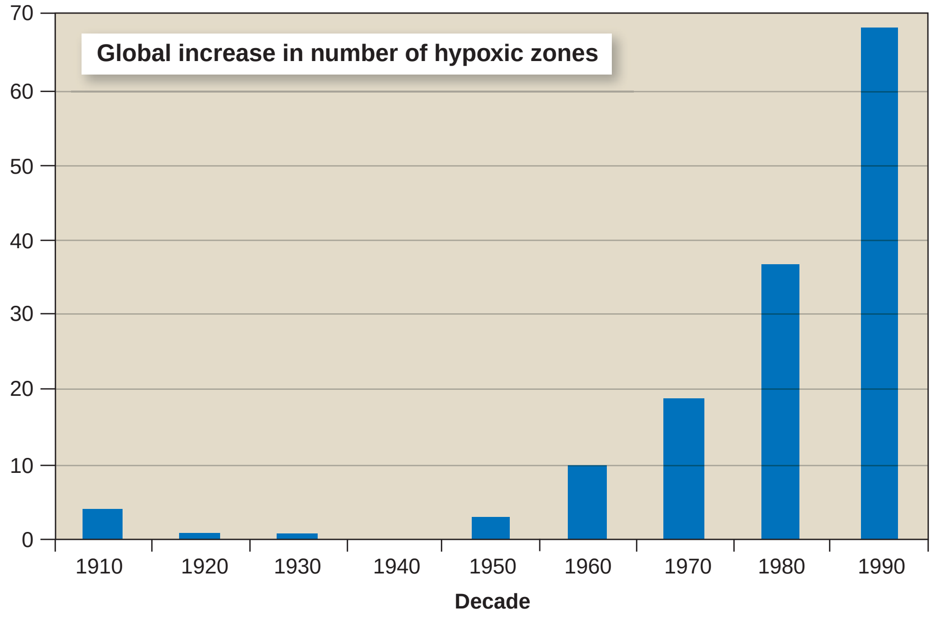


Figure 14 Global number of hypoxic zones by decade.

permanent areas in the ocean with greatly reduced oxygen levels. Hypoxic zones form when large amounts of phytoplankton and the organic matter they produce sink and decay in deeper water, using up the oxygen. Hypoxic zones are often called "dead zones," which is technically incorrect because some microbes and invertebrates prosper in the low oxygen levels. Nevertheless, fish and other organisms vacate the area—eels, lobsters, crabs, and other animals have even been known to crawl up on land to escape—and most animals that can't move away die. Hypoxic zones occur naturally, but are an increasing problem. Their number has doubled every decade since the 1960s (Fig. 14), and many are growing in size. The Gulf of Mexico hypoxic zone that forms in summer, when the warming of the sea surface blocks mixing of oxygen into deeper water, has roughly doubled in size since the mid-1980s, though it varies from year to year depending on the weather and other factors (Fig. 15).

Today's eutrophication-related hypoxic zones are confined to enclosed seas or coastal areas near river mouths, but this could change. Barring a major change in human emissions, nitrogen input to the open ocean from the atmosphere is predicted to increase dramatically by 2050. It is reasonable to expect that phytoplankton growth, currently limited in much of the ocean by nitrogen supply, will increase. We don't know what will happen next. If we're really lucky the enhanced phytoplankton growth might give a boost to fisheries and pull some CO_2 out of the atmosphere to reduce the greenhouse effect. On the other hand, we could "crap out" and create the mother of all dead zones.

The No-Zone

Ozone (O_3) is a reactive form of oxygen, much different from the ordinary molecular oxygen (O_2) we breathe. Ozone in the lower atmosphere is a health hazard and damages plants and buildings. High in the stratosphere, however, a natural layer of ozone shields life from ultraviolet radiation (UV), which causes skin cancer and eye damage in humans and may harm crops. UV is also suspected of biological impacts ranging from damage to phytoplankton and fish eggs to blindness in polar bears.

In the late 1970s scientists found that ozone levels in the stratosphere were declining, and in 1985 they discovered a huge "hole" in the ozone layer over Antarctica. From then on the Antarctic ozone hole has formed every year in September and October, steadily increasing in size (Fig. 16) despite fluctuating somewhat from year to year because of stratospheric weather. Much of the Southern Hemisphere is experiencing higher UV levels as a result. Less severe, but still worrying, ozone depletion has also occurred over the Arctic and at middle latitudes.

Chlorofluorocarbons (CFCs), synthetic gases that were widely used in spray cans and air conditioners, have caused most of the ozone depletion. CFCs released at the earth's surface gradually move up to the stratosphere, where they destroy the ozone. Nitrous oxide and other gases involved in the nitrogen cascade also contribute to ozone depletion. Ozone depletion is often confused with global warming because ozone, CFCs, and nitrous oxide are greenhouse gases, but the real issue regarding ozone is not rising temperature but a dangerous increase in UV levels.

CFCs have been largely phased out under a 1987 international agreement, the Montreal Protocol—gambling with UV was one bet the international community decided not to make. CFC emissions have been slashed, but CFCs released in the past are still making their way into the stratosphere. Though the size of the Antarctic ozone hole appears to be leveling off in the long run, it reached record proportions in 2006 and significant improvement is not expected until at least 2020.

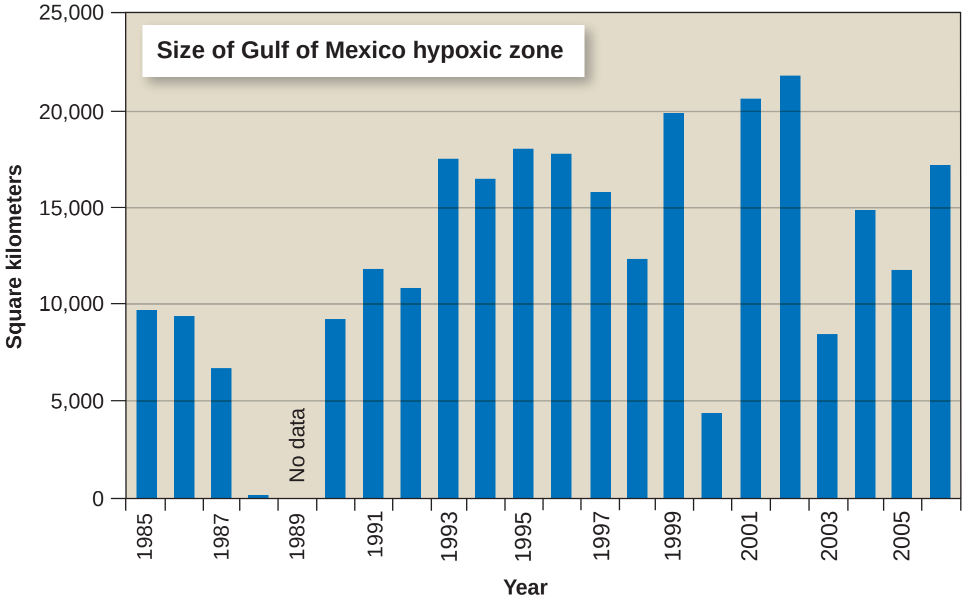


Figure 15 Maximum size of the hypoxic zone in the northern Gulf of Mexico by year.

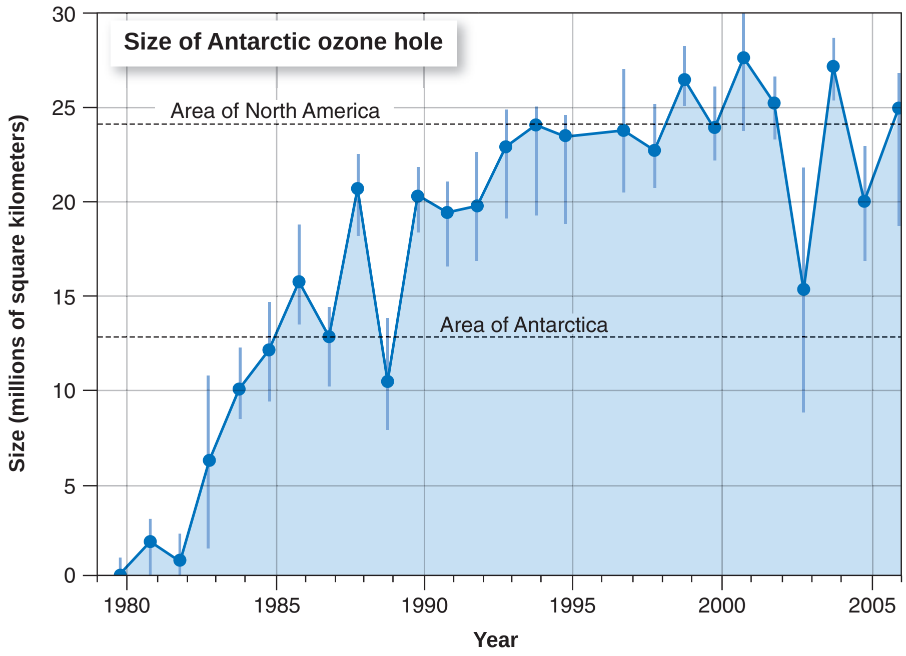


Figure 16 Average size of the Antartic ozone hole between September 7 and October 13, when the seasonal ozone hole is at its peak. The vertical bars represent the maximum and minimum size of the hole during this period.

So What Do We Do?

The only way we can avoid the worst impacts of global climate change is to take strong action as soon as possible. Every year of delay will eventually mean paying a higher "climate tax," and that even larger cuts in greenhouse gas emissions are needed to avoid disaster. The world might get lucky and discover a quick-fix technological solution to all our climate problems. Proposals so far range from the downright dangerous (like massively fertilizing the oceans in the hope that huge phytoplankton blooms will suck CO_2 from the atmosphere; see "Nutrients", p. 346) to the downright wacky (like sending huge mirrors into space to reflect solar energy). Until such a silver bullet comes along, averting dangerous climate change will require a whole range of actions (Fig. 17). Increasing energy efficiency and reducing wasteful consumption are the two biggest steps we could take, starting today. Other feasible steps include reducing subsidies on fossil fuel use, developing and investing in cleaner alternative technologies for power generation and transport, and reversing the loss of forests and wetlands. Another possibility is to store away, or sequester, CO_2 that we do generate, for example by locking it up in geological structures, but the technology to do this is unproven and CO_2 sequestration risks massive environmental impacts should the CO_2 escape into the atmosphere.

Countries have been slow to take the necessary actions. It wasn't until 1997 that nations at the Kyoto Climate Change Conference agreed to reduce emissions to 5.2% below 1990 levels by the year 2012. The agreement didn't come into force until 2004 when Russia became the 141st country to sign, bringing the emissions represented by signatory countries to 55% of total global emissions. Unfortunately, the United States, China, Australia, and some of the other biggest polluting countries pulled out of the agreement. Kyoto was only meant as an interim step in the first place and goes out of effect in 2012. So far, the diplomats have found it hard even to agree when to meet; there are few signs they will reach an effective agreement to cut global CO_2 emissions anytime soon.

"We can't afford to change," say climate-change critics, including some politicians. "It would cost jobs and prosperity, cripple our economy. Things will work out, nature takes care of itself." Those arguments no longer hold water. Yes, the changes needed to stabilize CO_2 emissions will cost money, a lot of money: an estimated 1–3% of the entire global economy every year through 2050. But even the maximum 3% investment to avoid the 5–20% climate tax would be a pretty good deal. It would also create more jobs, more prosperity, and a better economy. In fact, IPCC estimates that the investment needed to avert dangerous climate change would slow economic growth by no more than 0.12 percentage points. Many measures to reduce CO_2 emissions will have benefits of their own: More efficient power plants, electrical grids, homes, and cars will lower everybody's energy bills, and a reduced reliance on fossil fuels might improve political and economic stability.

Reduced fossil fuel use would reduce ocean acidification and global warming at the same time. Reactive nitrogen emissions would also be reduced, and rolling out existing technologies that reduce nitrogen emissions from fossil-fuel burning would also help. But reduced fossil-fuel burning, which accounts for only about 16% of reactive nitrogen emissions, won't be enough to fix the nitrogen cascade. Controlling the main sources of anthropogenic reactive nitrogen,

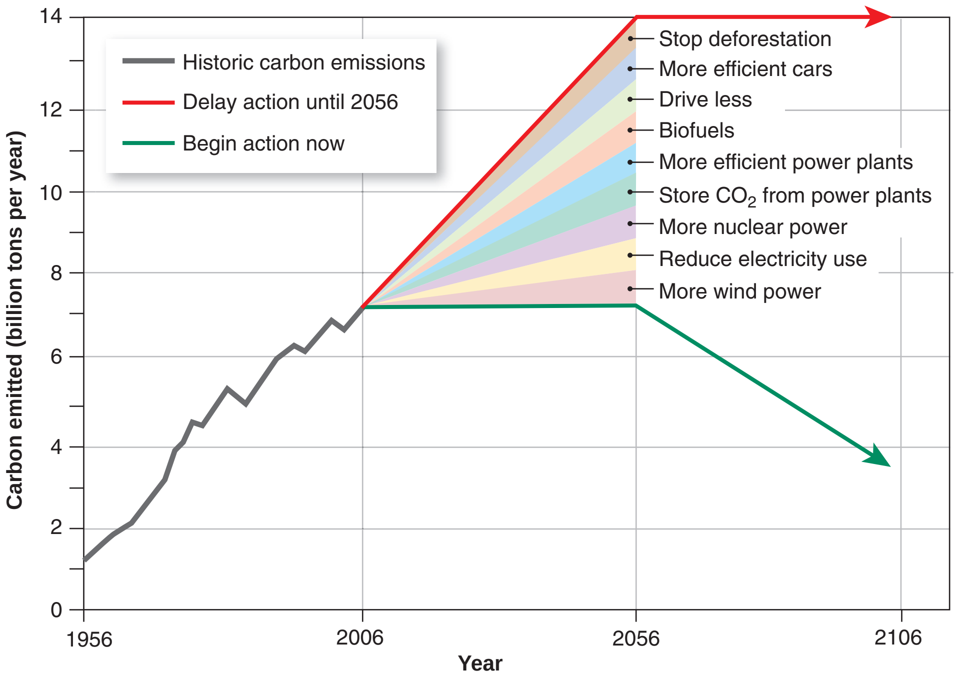


Figure 17 Some of the measures that can help stabilize global CO_2 emissions. Starting now means that emissions stablize at a lower level, and start to fall sooner than if we wait. No single measure can stabilize emissions. There are a number of possible measures in addition to those shown here.

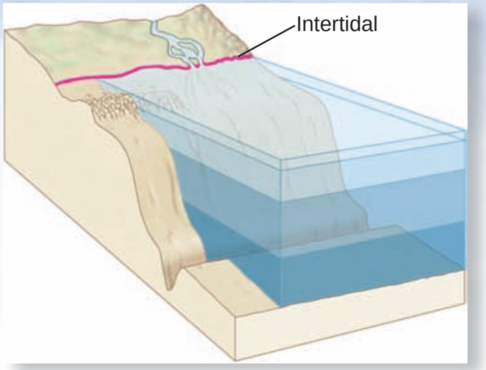
fertilizers and nitrogen-fixing crops, without compromising the food supply of a growing population, will be a major challenge. Research is needed on better ways to give plants only the nitrogen they need so there is no excess to run off into the environment, on better ways to manage livestock wastes, and on recycling rather than making new reactive nitrogen. Reducing government subsidies that encourage wasteful fertilizer use would also help. It is essential to maintain and restore habitats such as wetlands, estuaries, and bays that lock up both reactive nitrogen and carbon, and remove reactive nitrogen by denitrification. The restoration of streamside vegetation and wetlands in the Mississippi River basin, for example, is a key strategy to control the Gulf of Mexico "dead zone." Ultimately, international agreements are needed because reactive nitrogen flows across borders: Farmers and consumers in one country are reluctant to reduce their own emissions if nitrogen keeps flowing from other countries.

Global change skeptics often point to scientific uncertainties as an argument to wait for more information before doing anything. But using uncertainty as an excuse to delay action, when we do know beyond a reasonable doubt that the consequences of inaction are at least potentially catastrophic, is a colossal gamble. Yes, there are uncertainties, as there always are in science. It is worth remembering that much of the uncertainty about global change is because we are moving into uncharted waters beyond human experience. Uncertainty works both ways: The consequences of global change might be greater, not less, than scientists predict. Many scientists, in fact, feel that current predictions of future global change have been too conservative because of political pressure for a lowest-common-denominator consensus. Given the stakes, are you willing to roll the dice?

Rocky intertidal, Monterey Bay, California.

11
CHAPTER

Between the Tides



Of all the vast ocean, the intertidal zone, sometimes called the **littoral zone,** is the best known to marine biologists and laypersons alike. The intertidal zone is the narrow fringe along the shoreline that lies between the highest high and the lowest low tides. It is the only part of the marine world that we can experience firsthand without leaving our own natural element. We don't need a boat to visit the shore and, at least at low tide, we can see it without a face mask and move through it without swim fins. Perhaps more important from the scientist's point of view, we can work in the intertidal without cumbersome and expensive equipment and can easily return to the exact same place time after time. Intertidal communities are therefore among the most-studied and best-understood of all marine communities. Although the intertidal zone constitutes only a tiny fraction of the marine environment, lessons learned there have added immensely to our knowledge of marine ecology, and indeed of ecology in general.

The intertidal is unique among marine environments in that it is regularly exposed to the air. Organisms that live in the intertidal must have a way to cope with this exposure, even if it means giving up characteristics that would be advantageous below the tides. Being out of the water and exposed to air is called **emersion**—the opposite of **immersion,** or being submerged.

The effects of the tide, and thus the nature of the **community,** depend to a great extent on the type of bottom. The bottom—that is, the material on or in which an organism lives—is called

Community All the different populations of organisms that live in a defined area.
- Chapter 4, p. 71

the **substrate.** Hard, rocky bottoms are a very different **habitat** from soft bottoms made of mud or sand. In this chapter we consider intertidal communities on both kinds of substrate, beginning with the rocky intertidal. The major coastal communities of North America are shown on the foldout map at the end of the book.

The intertidal zone is the shoreline between the high and low tide marks. It is the only part of the marine world that faces regular exposure to air, or emersion. Intertidal communities differ greatly depending on whether they have rocky or soft bottoms.

ROCKY SHORE INTERTIDAL COMMUNITIES

Rocky shores generally occur on steep coasts without large amounts of sediment. Such areas have often been recently uplifted or are still rising as a result of geological events. These uplifted coasts have not had time to erode or accumulate sediment. The west coast of the Americas, for example, is largely rocky because its **active margin** has been uplifted by geological processes. Eastern Canada and New England were covered by huge sheets of ice during the last ice age (see "Climate and Changes in Sea Level," p. 33). The ice sheets scraped sediment from the continental shelf, exposing the bare rock underneath. Under the tremendous weight of the ice, the coast actually sank partially down into the **mantle.** When the ice melted, the coast slowly rose, or rebounded, leaving a coastline of exposed rock. Sea level, however, began to rise, and eventually the rise in sea level overtook the rebound of the coast. The sea flooded the rocky coast, forming the beautiful, deeply sculptured shoreline north of Cape Cod. This is the only part of the Atlantic coast of North America that has much rocky shore. The southern Atlantic and Gulf coasts of North America are slowly sinking, or **subsiding,** weighed down by huge amounts of sediment that are accumulating on the **passive continental margin.** Rocky areas are uncommon on these coasts.

Not all rocky shores are formed by uplift. Waves and currents can carry sediments away, leaving bare rock behind. Similarly, outcrops of hard, erosion-resistant rock may be left behind after softer surrounding rocks erode away. Much of the coast of the island of Hawai‘i is rocky because it is geologically very young. Formed by successive flows of lava into the sea, the coast hasn't had time to accumulate sediment. In fact, the coast is still being formed by the periodic eruptions of the Kilauea volcano (Fig. 11.1).

Rocky shores usually occur on recently uplifted or geologically young coasts or on coasts where erosion is removing sediments and soft rock. In North America, rocky shores are common on the west coast and on the east coast north of Cape Cod.

It is difficult to burrow through rock, though rock-boring clams (*Zirfaea, Penitella*) can do it in soft rock like sandstone. Most rocky intertidal organisms live right on the rock's surface. Animals that live on the surface of the substrate—be it rock, sand, mud, or even other organisms—are called **epifauna.** Some epifauna move about over the rocks, but many are **sessile** and stay attached to the rock.

Living on the rock's surface, the organisms in the rocky intertidal are fully exposed to the elements. This subjects them to great physical stress.

Exposure at Low Tide

Low tide presents problems for the organisms of the rocky intertidal. Left high and dry, they are exposed to the air, a much harsher environment than water. The higher the organisms live in the intertidal, the more time they have to spend out of the water. The upper part of the intertidal zone is only immersed at the peak of high tide and then only briefly. The very upper edge may not be submerged, and not every day during exceptionally high **spring tides.** The highest part of the "intertidal," in fact, is almost never immersed. It is kept wet by wave splash.

Organisms that live low in the intertidal, on the other hand, are submerged most of the time and have to cope with emersion only for short periods or, at the lowermost edge, only at the most extreme low tides.

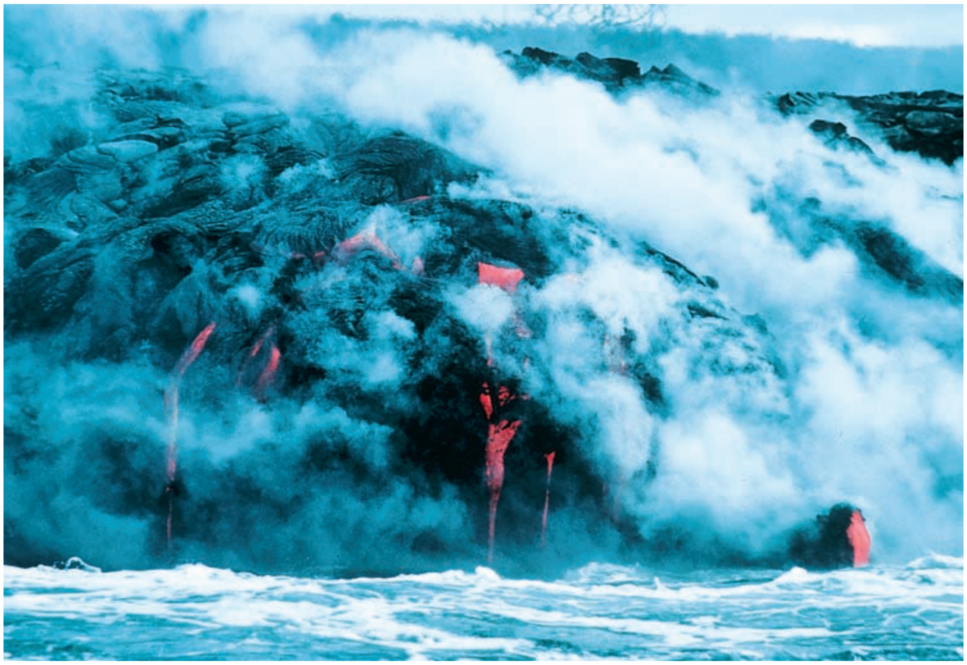


FIGURE 11.1 Lava flows are creating new rocky shorelines on the island of Hawai‘i.

Emersion time, or time spent out of the water, gets longer the higher in the intertidal you go.

Water Loss Marine organisms tend to dry out, or **desiccate,** when exposed to air. To survive in the intertidal, an organism must be able to prevent desiccation, tolerate it, or both. Most intertidal organisms cope with the problem of drying out in one of two basic ways: They either run and hide or they "clam up."

The run-and-hide strategy is simple enough. When the tide goes out, the organism goes somewhere wet and waits for the tide to come back in. It is not unusual to see shore crabs, hermit crabs, snails, and other rocky shore denizens huddled in moist, shady cavities or crevices in the rocks (Fig. 11.2). **Tide pools,** depressions in the rocks that hold seawater after the tide goes out, are favorite places to hide (Fig. 11.3). Some areas are kept moist by spray from waves or by water that slowly leaks out of tide pools. The hiding place may even be provided by other organisms (Fig. 11.4).

Seaweeds and sessile animals cannot run, but many are able to hide. Instead of moving to moist areas when the tide goes out, they live in moist areas all the time (Fig. 11.5). This may be because the larvae or spores settle only in moist, shady places or because those that settle elsewhere dry out and die.

Organisms that use the "clam-up" strategy have some sort of protective covering, like a shell, that they can close to hold in water. Some, like barnacles and mussels, are completely enclosed and can seal in moisture simply by closing their shell. Others, like limpets, have an opening that cannot

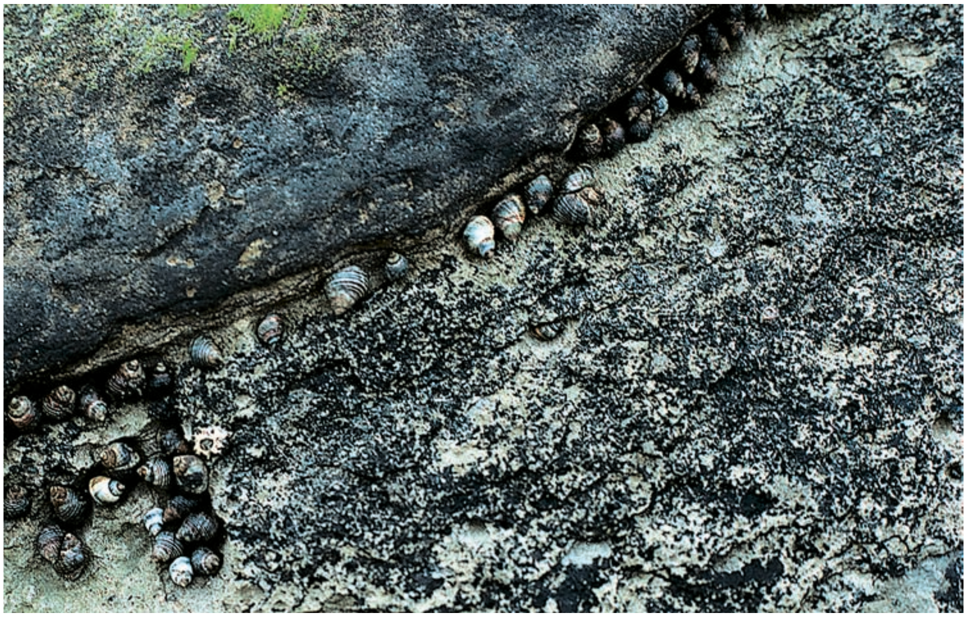


FIGURE 11.2 These periwinkles (*Littorina cincta*) get through low tide by clustering in a moist, shady crevice. They also seal against the rock to retain moisture.

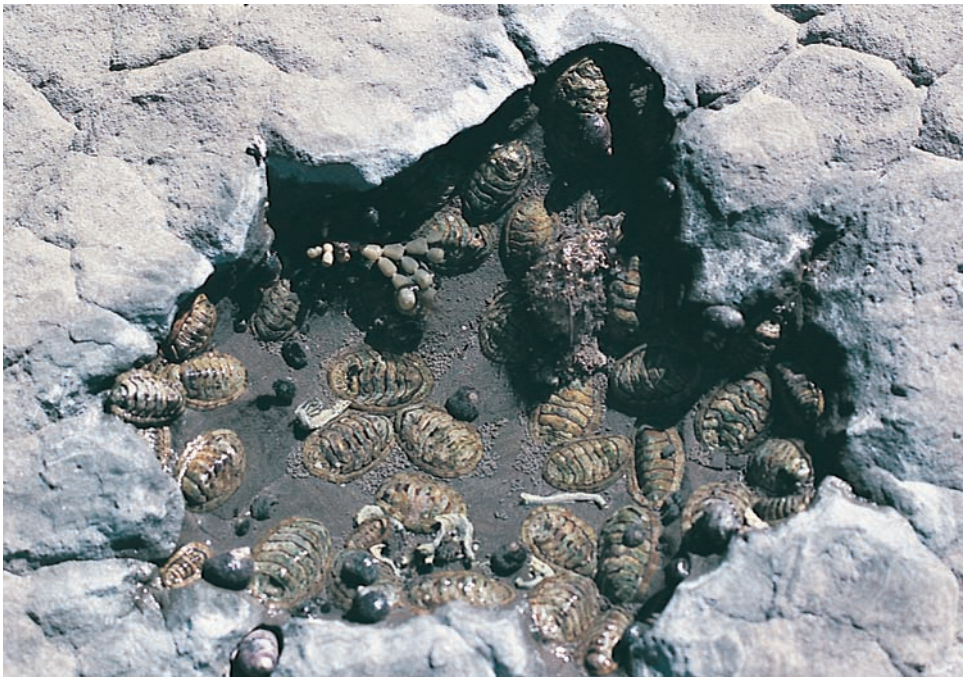


FIGURE 11.3 When the tide goes out, a little bit of the ocean stays in this small tide pool in New Zealand. Organisms like these chitons (*Sypharochiton pelliserpentis*) and snails (*Diloma atrovirens*) move to such pools to stay moist. Even in tide pools, however, life can be tough. The water often undergoes drastic changes in salinity, oxygen content, and temperature.

Habitat The natural environment where an organism lives.
- Chapter 2, p. 19

Active Continental Margin One that is colliding with another plate and therefore has a lot of geological activity.
- Chapter 2, p. 34; Figure 2.22

Mantle One of the three main internal layers of the earth. The mantle lies under the *crust,* the outermost layer, and over the *core,* the innermost layer.
- Chapter 2, p. 21; Figure 2.3

Passive Continental Margin One that is on the "trailing edge" of a continent and has little geological activity.
- Chapter 2, p. 35; Figure 2.22

Spring Tides Tides with a large range that occur around times of the full or new moon.
Neap Tides Tides with a small range that occur when the moon is in quarter.
Tidal Range The difference in height between a high tide and the next low tide.
- Chapter 3, p. 60

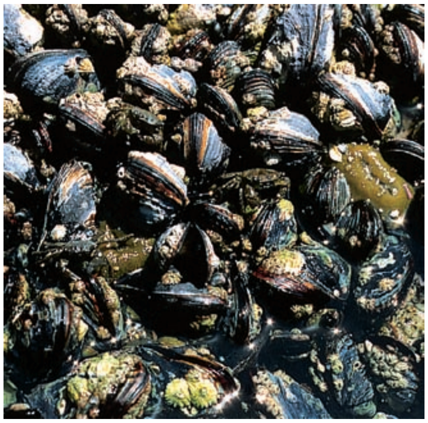


FIGURE 11.4 Mussels (*Mytilus californianus*) form dense clumps that retain moisture. This helps protect the mussels and provides habitat for smaller organisms.

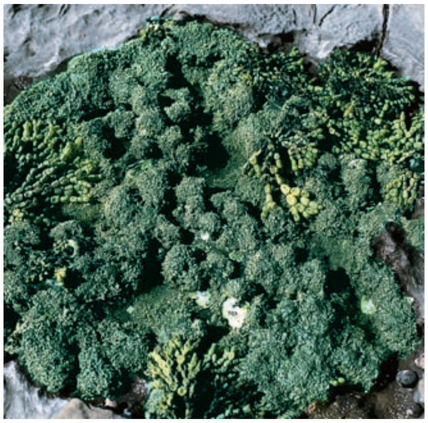


FIGURE 11.5 These seaweeds can't move to moist depressions at low tide, so they live there permanently. They don't grow on the surrounding rock because it dries out.

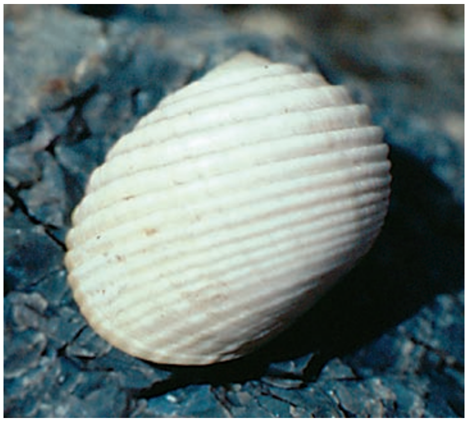


FIGURE 11.6 The shell ridges on this tropical snail (*Nerita plicata*) help it stay cool by radiating heat. The snail's white color probably helps by reflecting sunlight.

be completely shut. These organisms typically clamp themselves tightly to the rock to seal the opening. Some use mucus to make a better seal. They may also carve out shallow depressions, or "home scars," in the rock that make the seal more effective. They do this by scraping the rock with their shell or their **radula,** slowly wearing the rock away. Every strategy has disadvantages, however: Clamming up can make it harder for animals to obtain oxygen and food.

Some organisms use a combination of strategies. The periwinkles (*Littorina*) shown in Figure 11.2, for example, clamp themselves to the rocks to seal in moisture. They can also seal off the opening of their shell by closing the **operculum,** a stiff plate that fits the opening like a door. Periwinkles are still not immune to desiccation, however, so at low tide they congregate in moist, shady places, especially on hot, sunny days. Desiccation is a particular problem in hot, tropical climates, where intertidal organisms are often confined to tide pools or damp, shady spots.

Finally, some intertidal organisms use neither the run-and-hide nor the "clam-up" approach. Instead, they simply tolerate drying out. Some intertidal **chitons** can survive the loss of 75% of the water in their tissues. Some intertidal seaweeds, such as rockweeds (*Fucus;* see Fig. 6.5), can withstand a water loss of as much as 90%, becoming almost completely dry and practically crunchy. They quickly recover when the tide comes in and wets their tissues.

Some intertidal organisms avoid drying out by moving to or living in wet spots. Others can close a shell to retain water. Still others are able to dry out and then recover after the tide returns.

Temperature and Salinity Emersion creates problems other than desiccation for marine organisms. Sea temperatures are relatively constant and mild because of the high **heat capacity** of water, but air temperatures can be much more extreme. At low tide, intertidal organisms are at the mercy of the sun's heat and the freezing cold of winter. Because tide pools are shallow, they too experience extreme temperatures, though usually not as extreme as air temperatures.

Most intertidal organisms can tolerate a wide temperature range. Tide-pool fishes, for example, are much more tolerant of extreme temperatures than related fishes that live below the tides. Certain species of periwinkle from high in the intertidal show remarkable heat tolerance. One is known to survive temperatures as high as 49°C (120°F) in the laboratory.

Organisms deal with temperature extremes in ways besides simply being tough. Those that move to moist hiding places to avoid drying out, for example, also avoid high temperatures because such places tend to be cool as well as damp. Some snails, especially in the tropics, have pronounced ridges on their shells. Like the fins on a car radiator, these ridges help the snail lose excess heat (Fig. 11.6).

The color of a snail's shell can also help it tolerate high temperatures. Snails that are regularly subjected to extreme high temperatures tend to be light in color. The light color helps reflect sunlight to keep the snail cool. On Atlantic shores, for example, the dog whelk or dog winkle (*Nucella lapillus*) has two color forms: white-shelled and brown-shelled. On shores exposed to heavy wave action, brown whelks predominate. On sheltered shores the white form is most common. The difference appears to be related to temperature. Brown whelks absorb more heat than white ones and die in temperatures that don't seem to harm the white snails. On the exposed coasts where brown snails live, there are dense mussel beds, which stay moist (see Fig. 11.4) and relatively cool. Wave spray also helps cool the snails. Sheltered coasts have few mussels and little wave spray so they are hotter, and white whelks have an advantage.

Salinity also fluctuates widely in the intertidal. When it rains, exposed intertidal organisms have to endure fresh water, which is fatal to most marine organisms. Many simply keep the fresh water out by closing their shells—another benefit of the "clam-up" strategy. Even so, rainstorms during low tide sometimes cause the mass mortality of intertidal organisms.

Tide-pool residents, too, face extreme variation in salinity. At low tide, pools may be diluted by rain, lowering the salinity. On hot, dry days, salinity rises because of evaporation. To cope, tide-pool organisms can usually withstand a wide range of salinity as well as temperature. They may also burrow or reduce their activity to ride out extreme conditions and wait for high tide.

FIGURE 11.7 Ocean waves expend tremendous energy when they break on the shore.

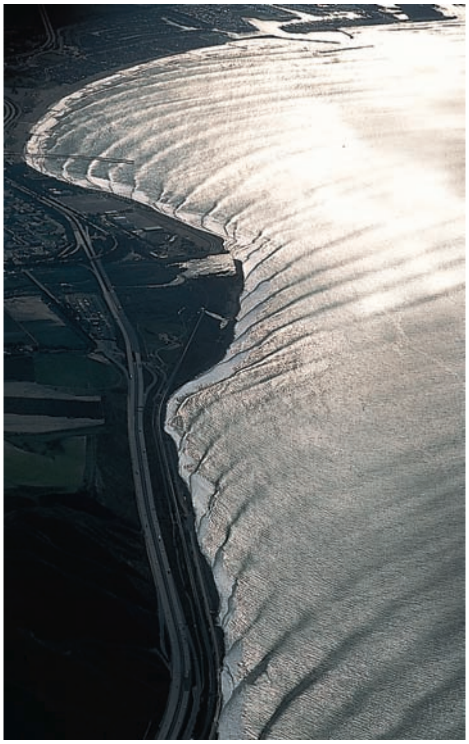


FIGURE 11.8 Nearly all waves approach the coast at an angle. As a result, they refract, or bend toward the coast. By the time the waves break they are almost parallel to shore.

The intertidal has more extremes of temperature and salinity than other marine environments because it is exposed to the air. Intertidal organisms have evolved various mechanisms to avoid or endure these extremes.

Restriction of Feeding Because little sediment accumulates in the rocky intertidal, **deposit feeders** are uncommon. Most of the sessile animals are **filter feeders.** They are unable to feed when the tide is out. For one thing, they have to be under the water to filter it. Furthermore, many of them "clam up" during low tide and can't extend their filtering or pumping apparatuses with their shells closed.

Even animals that are not filter feeders have trouble feeding at low tide. Many mobile animals in the rocky intertidal are grazers that scrape algae, bacteria, and other food from the rocks. Others feed on pieces of seaweed and other large **detritus** that drift in from deeper water. Some are predators and move over the rocks in search of prey. When mobile animals seek shelter or clamp to the rocks to avoid water loss at low tide they can't move around to find food.

Being unable to feed when the tide is out is not much of a problem for animals low in the intertidal. They are immersed most of the day and have plenty of time to feed. Higher in the intertidal, however, animals may not be underwater long enough to get adequate feeding time. This can cause them to grow more slowly or even prevent them from living in the high intertidal at all.

Many intertidal animals are unable to feed when exposed at low tide. This may prevent them from living higher on the shore than they do.

The Power of the Sea

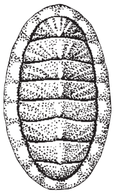
Even when the tide is in, life in the intertidal is not necessarily easy. Ocean waves expend tremendous energy as they crash on the shore. Anyone who has been knocked around by the surf appreciates how much energy waves can carry. Rocky intertidal organisms are exposed to the full power of the sea (Fig. 11.7).

The Distribution of Wave Energy along the Shore The impact of waves varies along the shoreline. Some areas are sheltered from the surf; others are fully exposed. Enclosed bays, for example, are usually protected from wave action, which is why they are used for harbors. It is not always easy to predict which areas will be sheltered and which exposed, however.

Recall from Chapter 3 (see "Waves," p. 55) that when a wave enters shallow water it "feels" the bottom and slows down. Thus, the same wave travels faster in deep than in shallow water.

Waves almost never approach the shore straight on, but instead come in at an angle (Fig. 11.8). One "end" of the wave reaches shallow water before the other. The end in shallow

Radula A rasping ribbon of small teeth that is present in most molluscs.
- Chapter 7, p. 129; Figure 7.21 inset



Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface.
- Chapter 7, p. 129

Heat Capacity The amount of heat energy required to raise the temperature of a substance; also, its ability to hold heat. Water has one of the highest heat capacities of any natural substance.
- Chapter 3, p. 42

Deposit Feeders Animals that eat organic matter that settles to the bottom.
Filter Feeders Animals that actively filter food particles from the water. They are a common type of *suspension feeder.*
- Chapter 7, p. 116; Figure 7.1

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

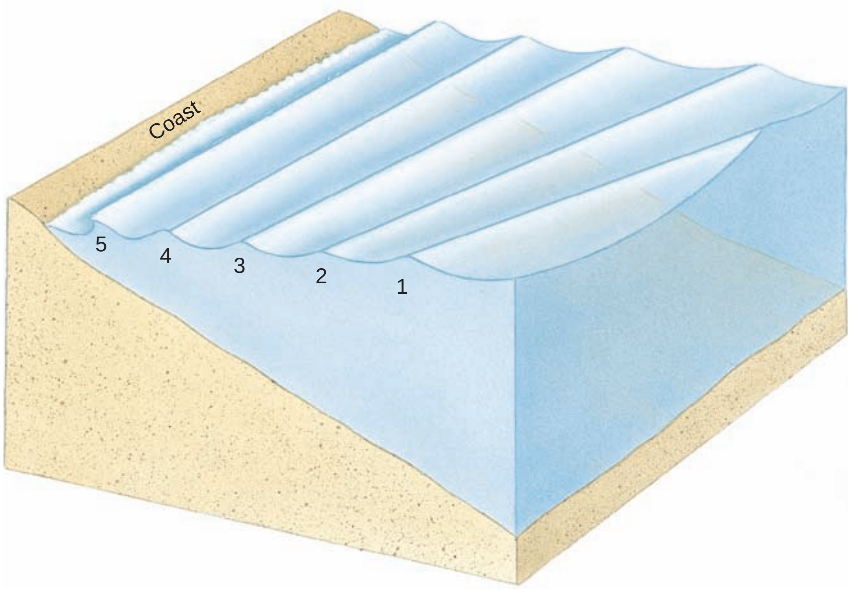


FIGURE 11.9 Wave refraction. Wave crests can be represented by lines on a diagram. Here the lines indicate the crest of a single wave at successive times. At time 1, the entire wave is in deep water. At time 2, the left end of the wave has entered shallow water and slows down, but the right end is still in deep water. As a result, the wave bends to become more parallel to the shore. This process continues so that the wave is nearly, but not quite, parallel to shore when it breaks (time 5).

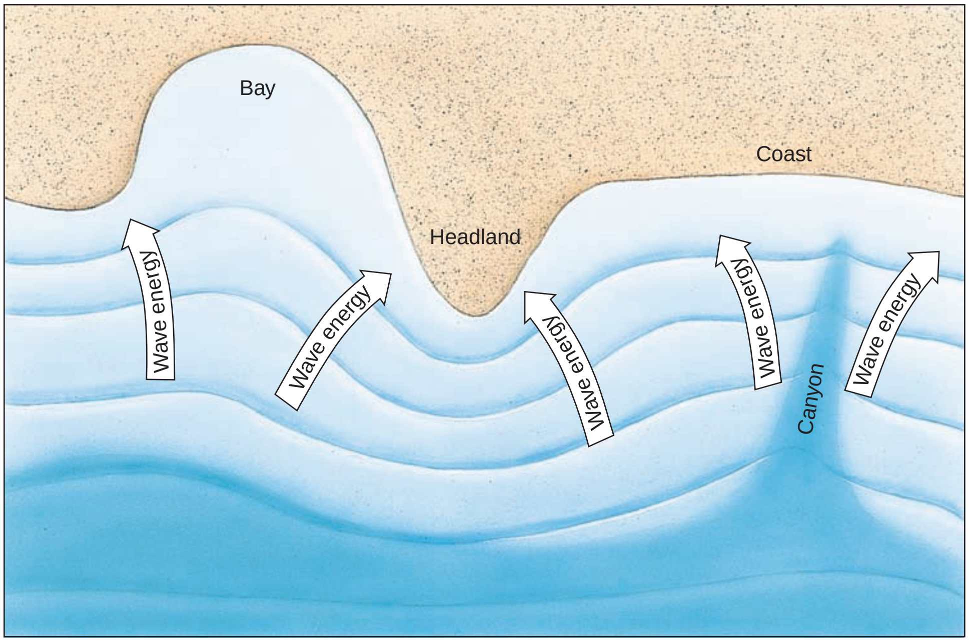


FIGURE 11.10 Both the coastline and bottom affect wave refraction. For example, an incoming wave first hits shallow water straight out from a headland. This part of the wave slows, lagging behind the sections on either side. As a result the wave wraps around the headland, which gets most of the wave shock. Just the opposite occurs in bays or over submarine canyons: The central part of the wave is in the deepest water, and the wave turns off to both sides. This deflects wave energy away from the bay or the shore behind the canyon.

water slows down, but the end in deep water continues to travel at its original speed. As a result, the wave bends, just as a two-wheeled cart will turn to one side if a wheel sticks. This bending of the wave, called **refraction,** causes the waves to become nearly parallel to the shore (Fig. 11.9). They never quite get perfectly parallel, however.

Refraction produces complex wave patterns when the coast is not a straight line. In particular, wave action tends to focus at headlands (Fig. 11.10). Bays, even if they are not physically sheltered from incoming waves, generally get less wave energy.

Incoming waves refract, or bend, to become more parallel to the shore. This increases wave impact at headlands and decreases it in bays.

Offshore bottom features can influence the effect of waves on the coast. Submarine canyons, for example, may cause wave refraction. Also, waves often break on reefs or sand bars and expend their energy before they reach the shore.

The result of all this is that there is tremendous variation in the intensity of wave impact, or **wave shock,** from place to place along the shore. Exposure to waves strongly affects intertidal organisms (Fig. 11.11).

Coping with Wave Shock Some intertidal organisms simply can't withstand wave shock and are found only in sheltered locations. Such species are often delicate or unable to keep a firm grip on the rocks. Because sediment tends to accumulate in the sheltered spots where they live, these organisms often cope with sedimentation better than those that live on exposed shores.

Organisms exposed to the waves need some way to deal with wave shock. Sessile organisms anchor themselves firmly to the rocks to keep from being washed away. Seaweeds use their **holdfasts** or simply encrust on rocks. Barnacles secure themselves with a glue so strong that several companies tried to duplicate it. Mussels attach with their **byssal threads,** strong fibers made of protein that the mussel produces with a special gland in its foot. These threads form the mussel's "beard." Though we usually think of them as stationary, mussels can slowly move about by putting out new threads and detaching old ones.

Mobile animals, too, often cling strongly to the rocks. Limpets and chitons, for example, use their muscular foot like a powerful suction cup. Gobies (*Gobius*) and clingfishes (*Gobiesox*), which are common tide-pool fishes, also have suction cups, formed by modified pelvic fins. The fishes don't stick as strongly as limpets, but unlike limpets they can swim home if dislodged. Intertidal fishes also tend to lack **swim bladders,** so they sink and stay on the bottom.

Rather than resist the waves, many intertidal animals find shelter when wave action gets too strong. This is especially true of highly

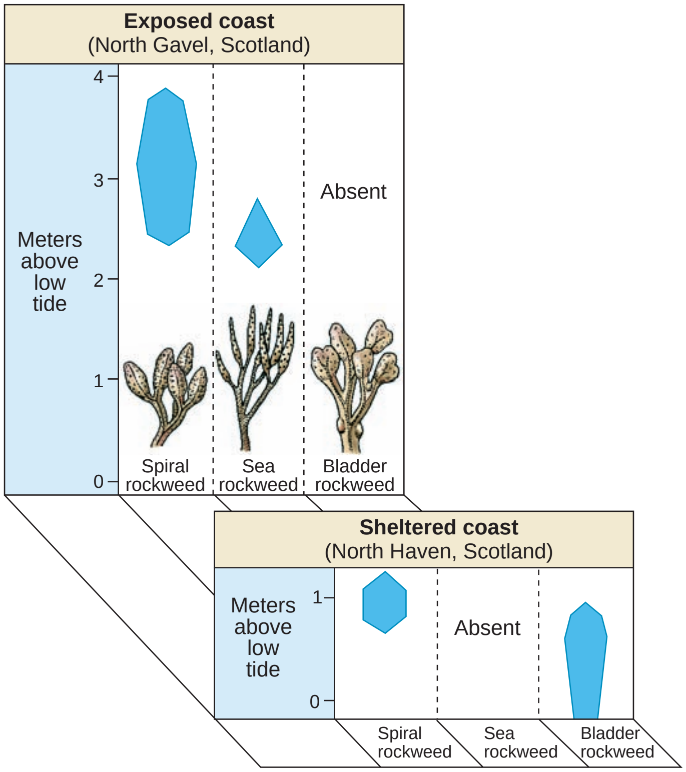


FIGURE 11.11 Even closely related species may be affected differently by wave exposure. On the Scottish coast the bladder rockweed (*Fucus vesiculosus*) occurs only in sheltered locations, the sea rockweed (*F. inflatus*) only at exposed sites. The spiral rockweed (*F. spiralis;* see Fig. 6.5) occurs in both environments but lives higher up on the exposed coast. This is probably because wave splash reaches higher at exposed locations. Such differences may be caused by the effects of waves on competitors or predators rather than the direct effects of wave shock. Diagrams like this are known as "kite diagrams." A wider blue "kite" indicates that more individuals of that species are at that elevation above low tide.

mobile animals like shore crabs (*Pachygrapsus, Grapsus*). In fact, there may be a trade-off between being able to move fast and having a strong grip on the rocks. Holding on tightly tends to slow an animal down. Many intertidal snails are easier to knock from the rocks when they are moving around than when they stop and clamp down. Not surprisingly, they usually stop and hold on when wave action is heavy. This limits their feeding, which prevents some species from living in highly exposed areas.

Intertidal organisms have other adaptations to withstand wave shock. Animals in exposed locations tend to have thicker shells than those in sheltered ones. A compact shape can also help reduce the impact of the waves (Fig. 11.12). Many intertidal animals, including barnacles, mussels, limpets, and chitons, have low profiles close to the rocks. Colonies of the sand-castle worm *Phragmatopoma californica* provide another example of the importance of shape. These colonies are not especially strong and are easily crushed, but they can withstand considerable wave shock because of their domed shape. Some organisms, especially seaweeds, are flexible and can "go with the flow" (Fig. 11.13). There may also be safety in numbers (Fig. 11.14).

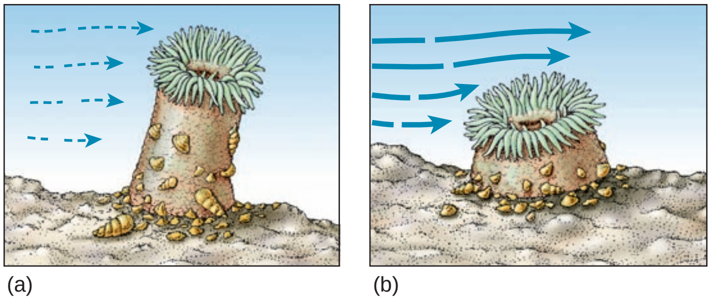


FIGURE 11.12 The giant green sea anemone (*Anthopleura xanthogrammica;* see Fig. 11.26) lives low in the intertidal zone on the Pacific coast of North America. (*a*) In sheltered locations the anemone grows relatively tall. (*b*) Anemones from areas with heavy wave action are much shorter. This reduces the body area that is exposed and allows more water to slide over the top of the anemone. In other words, drag is reduced.

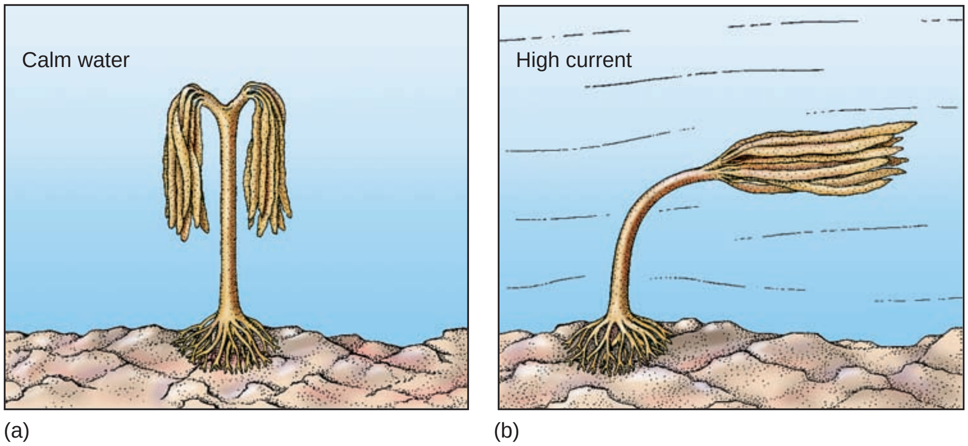


FIGURE 11.13 Organisms like this brown alga, the kelp *Eisenia arborea,* withstand waves by being flexible. (*a*) In calm water the plant stands upright. (*b*) When a wave hits, the plant bends over and the fronds fold up. This streamlines the plant and reduces water resistance.

Organisms on exposed coasts deal with wave shock in different ways, including strong attachments, thickened shells, low profiles, and flexibility.

Even the firmest grip on the rocks is of little help if the wave smashes a loose rock or drifting log into the rocks, crushing whatever is there. Waves can also turn rocks over, even large boulders. When this happens the organisms on top of the rock may be smashed or buried, and sunlight for the algae is blocked. The underside of the rock supports different organisms

Holdfast A structure used by many seaweeds to anchor themselves to the bottom.
- Chapter 6, p. 103; Figure 6.1

Swim Bladder A gas-filled sac that provides many bony fishes with buoyancy.
- Chapter 8, p. 157; Figure 8.12

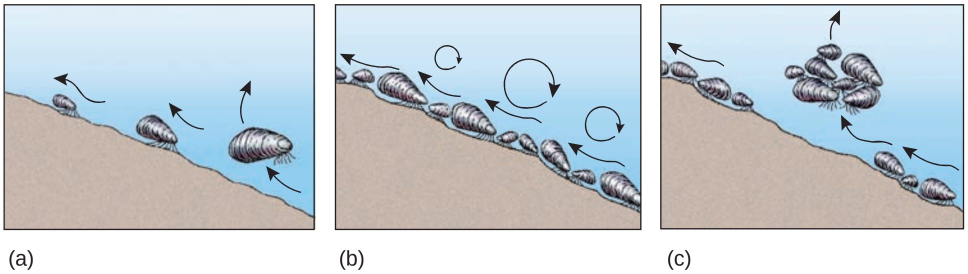


FIGURE 11.14 Intertidal animals may get some protection from wave shock by growing in dense groups. (*a*) Mussels (*Mytilus*) growing as isolated individuals, for example, get the full impact of the waves. Small individuals, which are closer to the rock, may be able to hang on but larger mussels, with more exposed surface area, can be torn away. (*b*) When the mussels grow in dense clusters, the waves do not get a direct shot at any of them but slide over the tops. Eddies created as the water flows over the mussels may also hold plankton near the mussels, increasing their food supply, and the dense clumps retain moisture at low tide. (*c*) If the clumps get *too* dense, however, many of the mussels attach to other mussels instead of the rock. Waves can cause more strain than the mussels on the bottom can bear and rip away entire clumps. This opens up space for other organisms, including other mussels.

than the top, and these fare no better. Once nestled comfortably under the rock, they are suddenly exposed to sun and waves, not to mention hungry predators. The organisms on both the top and bottom of overturned rocks usually die. People can have the same effect. If you happen to look under rocks at the shore, don't forget to turn them back over the way you found them.

Not only does wave action vary from place to place, organisms differ in how they are affected by waves. The result is that sheltered and exposed areas have very distinct communities. Marine communities in quiet bays are much different from those at exposed headlands. The effect of wave action can also be seen on a smaller scale: The organisms in a sheltered crevice usually differ from those on exposed rocks nearby.

The Battle for Space

Despite the intertidal zone's physical extremes, intertidal organisms generally have plenty of food. The high light levels and nutrient-rich coastal waters supply the basic requirements for **photosynthesis,** so there is vigorous algal growth. High tide also brings in abundant plankton as well as drifting seaweed fragments and other detritus (Fig. 11.15), which is actually the most important food source in many rocky intertidal communities. Limpets, snails, and other small, slow moving animals that graze algae from the rocks are often limited by food availability because they are unable to range over a wide enough area. For most other intertidal animals, particularly sessile ones, food is not usually a **limiting resource,** though feeding time can be restricted near the upper end of an animal's range.

Unoccupied space, on the other hand, is often in short supply. Even in sheltered areas intertidal organisms will drift away or be smashed on the rocks if they can't attach to the substrate. Sessile organisms need a permanent place to attach. Often there is not enough room to go around, and the availability

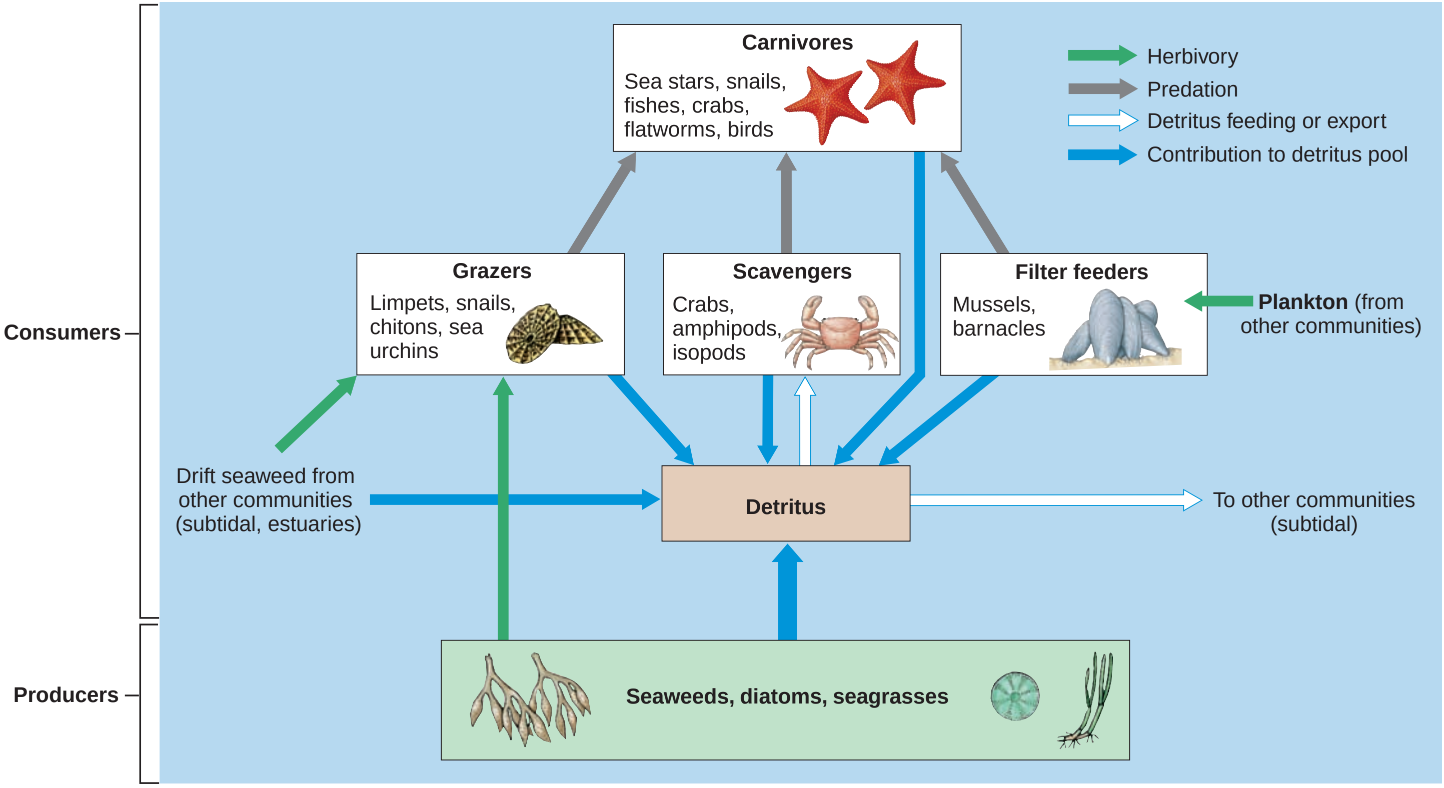

Carnivores
Sea stars, snails, fishes, crabs, flatworms, birds
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Grazers
Limpets, snails, chitons, sea urchins
Scavengers
Crabs, amphipods, isopods
Filter feeders
Mussels, barnacles
Plankton (from other communities)
Consumers
Drift seaweed from other communities (subtidal, estuaries)
Detritus
To other communities (subtidal)
Producers
Seaweeds, diatoms, seagrasses

FIGURE 11.15 A generalized food web on a rocky shore.

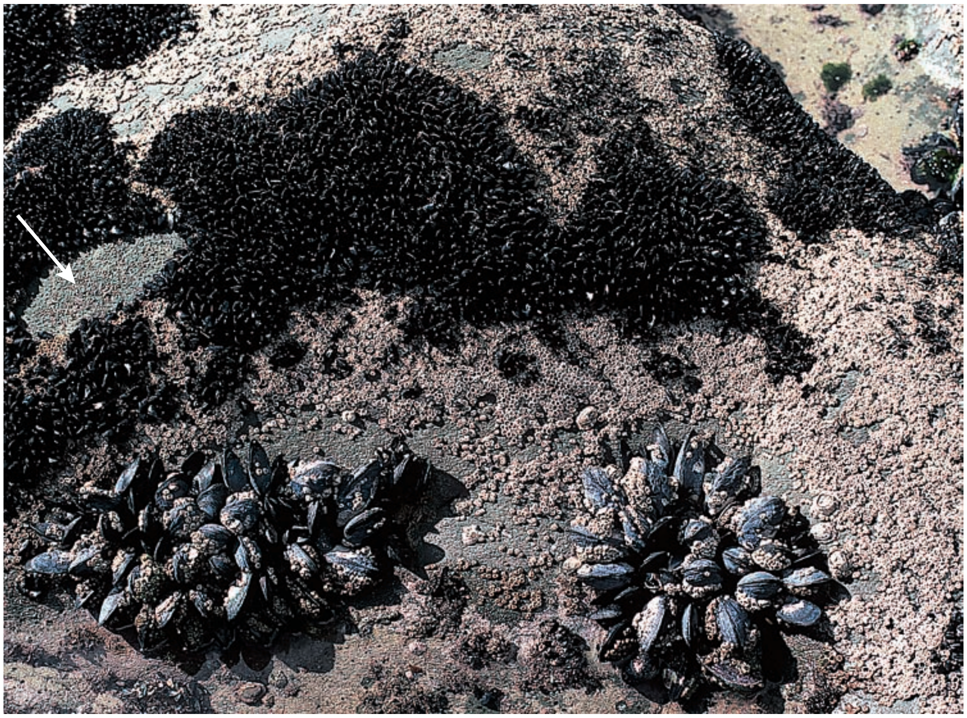


FIGURE 11.16 Most organisms in the intertidal zone live attached to the rocks, and most of the available space is occupied. This little patch of rock supports two species of mussels and two of barnacles, plus limpets and sea anemones. What little open space there is doesn't last for long: A small bare patch (arrow) has already been colonized by newly settled barnacles.

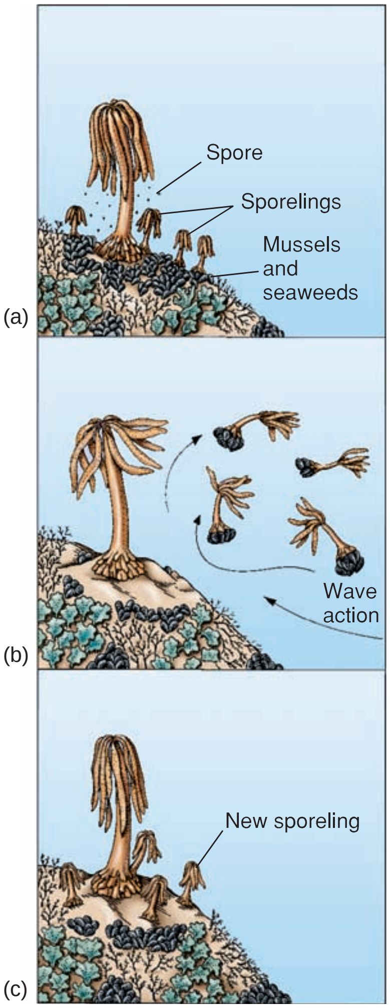


FIGURE 11.17 The sea palm (*Postelsia palmaeformis;* see Fig. 6.7) takes advantage of wave action to compete for space. (*a*) Adults literally drip spores, which develop into young sporelings near the parent. (*b*) When the space below is occupied, the sporelings grow on these competitors, which are eventually pulled from the rocks. (*c*) This clears space for a new generation of young sea palms.

of space commonly limits rocky intertidal populations. Nearly all the space in the intertidal is occupied (Fig. 11.16), and colonizers quickly take over what open space there is. Space is so scarce that organisms may attach to each other instead of to the rocks.

> Rocky intertidal populations are often limited by space, not food or nutrients.

Not surprisingly, competition for space is a dominant biological factor in the rocky intertidal. There are many ways to compete for space. One is to be the first to get to open spots. For intertidal organisms, this means having an effective means of **dispersal;** that is, organisms that depend on being the first to occupy new patches of open space must be good at getting themselves or their offspring from place to place. Most rocky intertidal species disperse via larvae or spores, which settle on the rocks to colonize open space. Having taken over the space, the organism must either be good at holding on to it or be able to reproduce rapidly to disperse its young to the next opening. Both strategies are used in the intertidal.

Rather than colonizing open patches, some intertidal organisms take over space that is already occupied. Barnacles, for instance, undercut their neighbors, loosening them from the rock. Owl limpets (*Lottia gigantea*) maintain a territory by bulldozing out intruders. Less forceful methods may also work. Many intertidal organisms simply grow over their competitors, making them vulnerable to waves (Fig. 11.17), smothering them, or in the case of seaweeds, blocking precious sunlight. Some species grow in colonies, gradually increasing the amount of space they hold as the colony grows.

Two species of mussel provide an example of how competition and physical factors can interact to determine the distribution of organisms. On the west coast of North America the blue mussel (*Mytilus galloprovincialis;* also called the Mediterranean or bay mussel)

Photosynthesis

$CO_2 + H_2O$ + sun energy → organic matter + O_2
(glucose)

- Chapter 4, p. 66

Limiting Resource A resource that is so scarce that it restricts the growth of a population.

- Chapter 10, p. 213

is found mainly in sheltered locations, whereas the California mussel (*M. californianus*) is found on the wave-exposed open coast. As you might expect, the California mussel has a thicker shell and attaches more strongly to the rocks than the blue mussel. On the other hand, the blue mussel does just fine on open coasts as long as the California mussel is absent. The blue mussel is apparently rare on open coasts not because it can't take the waves but because it is out-competed by the California mussel. The California mussel, with its thicker shell, crushes the blue mussel when the two grow together. On the other hand, the blue mussel, unlike the California mussel, tolerates a lot of silt and can therefore survive in calm bays.

Vertical Zonation of Rocky Shores

Rocky intertidal communities vary markedly from place to place, but there is one feature that is remarkably constant. The rocky intertidal community is usually divided into distinct bands, or **zones,** at characteristic heights in the intertidal (Figs. 11.18 and 11.19). Thus, a given species is usually not found throughout the intertidal, but only within a particular vertical range. Biologists call this pattern of banding **vertical zonation.**

When the shore consists of an evenly sloping rock face, the zones are often sharply defined belts that can be easily distinguished by the colors of the organisms (Fig. 11.18). Many shores are much more uneven, with scattered boulders, channels, and gullies. Zonation may not be as obvious in such areas, but it usually exists nonetheless.

Marine biologists have spent a lot of time and energy studying the causes of vertical zonation. Though there is still much to be learned, we now know that zonation results from the complex interaction of physical and biological factors. A general rule is that the upper limit at which a species occurs is usually determined mainly by physical factors, whereas the lower limit is usually determined by biological factors, especially predation and competition.

Most rocky shores have a distinct pattern of vertical zonation. The upper limit of a zone is often set by physical factors, the lower limit by biological ones.

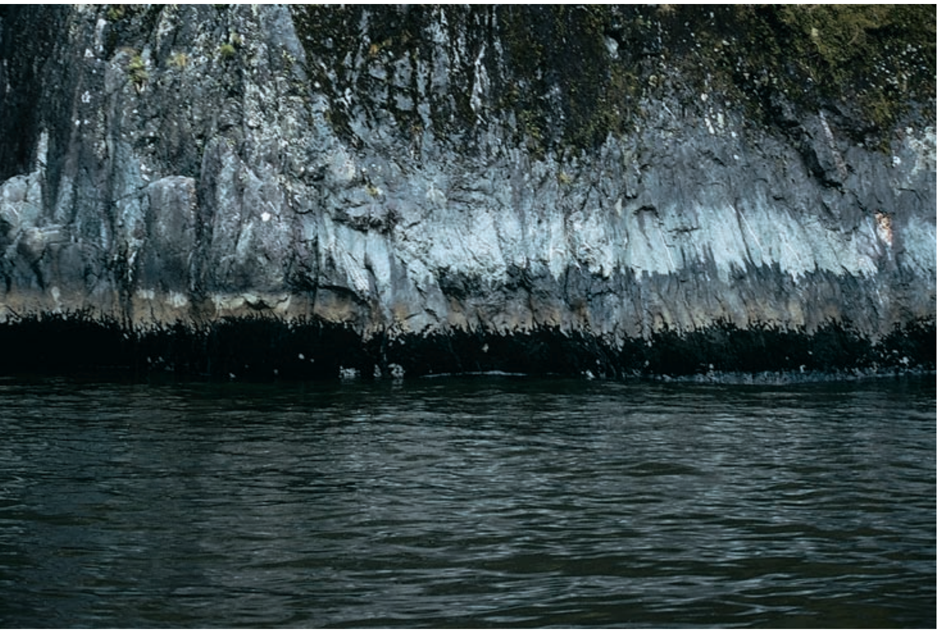
This rule is a useful starting point in understanding the causes of vertical zonation. As with all generalizations, however, there are exceptions. For example, zonation can be produced if the larvae of a species settle only at a particular height on the shore. One cannot just *assume* that the upper limit of a certain species is set by physical factors. Instead, this hypothesis must be *tested* by experiment (see "Transplantation, Removal, and Caging Experiments," p. 252). Furthermore, different factors often interact to determine the limits, and sometimes the line between physical and biological factors is fuzzy. As noted previously, for example, some filter feeders do not live high in the intertidal because they are not submerged long enough to feed. Is this upper limit due to a physical factor—emersion by the tide—or a biological one—feeding?

Many rocky shores around the world show a pattern of vertical zonation that is quite similar in its general nature but highly variable in its particulars. Biologists studying a certain area sometimes name the zones after the dominant organism, as in the "limpet zone" or the "mussel zone." These zones actually contain a variety of organisms. The mussel zone, for example, is also home to worms, crabs, snails, seaweeds, and many other species. Also, the specific organisms found in the intertidal vary from place to place. On the east coast of North America, for example, the mussel zone is often replaced by a rockweed zone.

Instead of naming the zones after organisms, we will simply divide the intertidal into the *upper, middle,* and *lower zones.* While not especially informative or creative, at least these names apply everywhere! Bear in mind that the following sections are general descriptions of "typical" intertidal communities and don't apply exactly to any particular place. Furthermore, the boundaries between zones are not absolute and some species occur in more than one zone. The next time you go to the shore, think about how these descriptions apply. Perhaps more importantly, think about how the place you visit is different. What might cause the differences?

The Upper Intertidal Seldom submerged, the inhabitants of the upper intertidal zone must be well adapted to withstand exposure to air. This zone actually lies mostly above the high tide mark, and the organisms are wetted mainly by wave splash and spray. It is often called the "splash zone." On exposed coasts with more wave splash the upper intertidal extends further above the high tide line than on sheltered coasts.

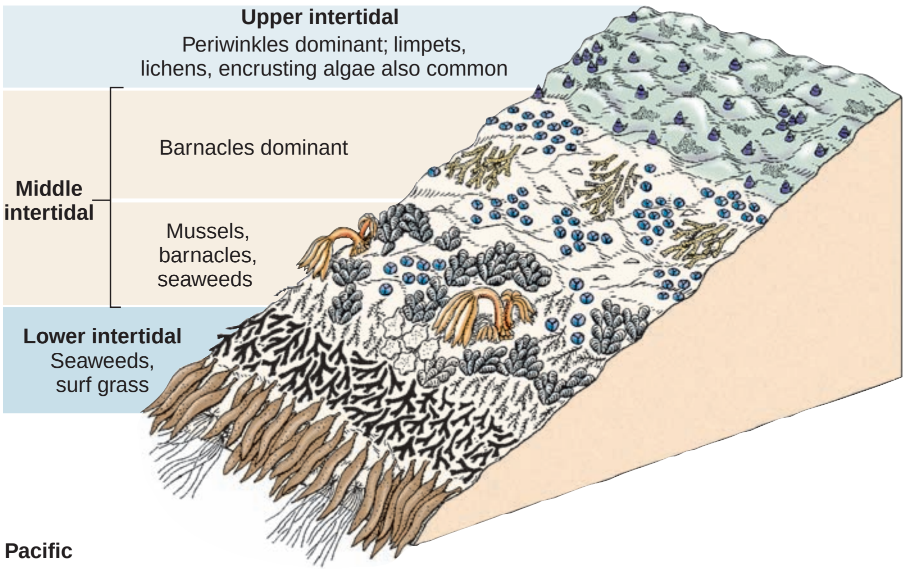
FIGURE 11.18 Intertidal organisms often form distinct bands, or zones, at different heights on the shore.



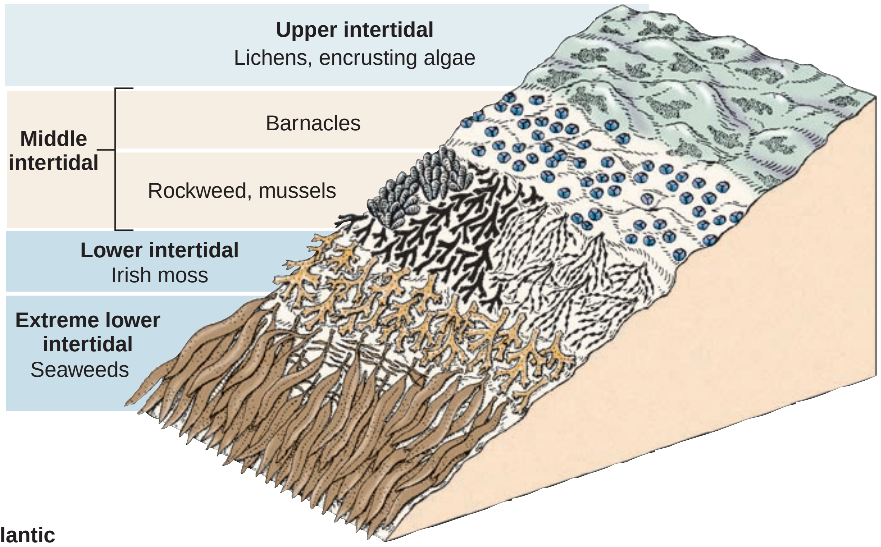
In many places, **lichens** (*Verrucaria*) form black, tar-like blotches on rocks in the upper intertidal. The fungus part of the lichen soaks up water, storing it for long dry periods. Dark green mats of cyanobacteria (*Calothrix*) are abundant. They are protected from drying out by a jelly-like coating and have the advantage of being able to **fix nitrogen** from the air. Small tufts of a filamentous green alga (*Ulothrix*) that is also resistant to drying out may spring up here and there. Other green (*Prasiola, Enteromorpha*), brown (*Pelvetia*), and red (*Porphyra, Bangia*) algae are occasionally found in the upper intertidal, usually in moist spots.

Large numbers of periwinkles graze on the algae, scraping it from the rocks with their radulas. Periwinkles (*Littorina*) are so abundant that the upper intertidal is often called the "*Littorina* zone." Not all of the many species of periwinkles live high in the intertidal, but those that do are well adapted to it. They can breathe air like land snails, live out of water for months, and tolerate extreme temperatures. They do have limits, however, and may have to seek shelter on hot days (see Fig. 11.2).

Limpets (*Acmaea, Lottia*) may also be found in the high intertidal. Like periwinkles, limpets are hardy grazers. Shore crabs occasionally venture into the upper intertidal, scurrying over the rocks. They mostly scrape algae off the rocks with their claws, but they may also eat animal matter, dead or alive. Sea lice or sea roaches (*Ligia;* see Fig. 7.33) breathe air and live above the water's edge, moving into the upper intertidal at low tide.


Upper intertidal
Periwinkles dominant; limpets, lichens, encrusting algae also common
Middle intertidal
Barnacles dominant
Mussels, barnacles, seaweeds
Lower intertidal
Seaweeds, surf grass

(a) **Pacific**



(b) **Atlantic**

FIGURE 11.19 Generalized patterns of zonation on temperate rocky shores on the (*a*) Pacific and (*b*) Atlantic coasts of North America. At any particular place on the coast the exact pattern will probably be different. Only organisms that characteristically dominate the various zones are shown. Hundreds of other species live in the intertidal.

Most of the upper intertidal zone lies above the high tide line and is kept wet by wave splash. The dominant primary producers are lichens and cyanobacteria. Periwinkles are the most common animals.

Few marine predators can reach the upper intertidal. Shore crabs occasionally eat periwinkles and limpets. From time to time predatory snails, such as unicorn shells (*Acanthina*), may also venture into the splash zone. On the other hand, the upper intertidal is often visited by predators from land. Birds such as oyster-catchers (*Haematopus*) may eat large numbers of limpets and snails. Raccoons, rats, and other land animals are also known to enjoy these tasty molluscs, as do people in most of the world.

The Middle Intertidal Unlike the upper intertidal, which is affected only by wave splash and the highest spring tides, the middle intertidal is submerged and uncovered by

Lichens Close, *mutualistic* associations between fungi and microscopic algae; mutualism is a type of *symbiosis.*

- Chapter 5, p. 99; and Chapter 10, p. 217

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.

- Chapter 5, p. 93; Table 5.1

Primary Producers Organisms that manufacture organic matter from CO_2, usually by photosynthesis.

- Chapter 4, p. 68

Transplantation, Removal, and Caging Experiments

A general principle in the intertidal zone is that physical factors, especially desiccation, usually determine how high in the intertidal a particular organism can live. Biological factors such as competition and predation set the lower limit. Where does this principle come from? How can you tell why a certain species of barnacle or seaweed is found where it is?

Like many scientific questions, this one is best answered by experiment—altering natural conditions to see what happens. In the intertidal, three general types of experiments have been particularly effective. In one of these, organisms are **transplanted** from one place to another to see whether they can survive under the new conditions. In one such experiment barnacles were grown on panels that could be placed at various heights on intertidal pier pilings. The barnacles soon died if they were moved higher than they normally lived. Measurements of their body fluids showed that they had lost a lot of water, so the cause of death was probably drying out at low tide. The experiment showed that the barnacles cannot survive the conditions above their normal range. Thus, their upper limit is set by a physical factor—desiccation.

Transplantation can also tell us when physical factors are not important. When barnacles are transplanted lower in the intertidal than they normally live, they do just fine. The same is true of many other intertidal species, including certain mussels, snails, and seaweeds. In fact, some species actually grow faster when moved below their normal range. Their lower limit, therefore, is not set by the physical environment.

If organisms can live lower in the intertidal, why don't they? Experiments suggest that other organisms, either competitors or predators, often set a species' lower boundary. In **removal experiments,** one species is removed from an area, which is then compared to an untouched **control** area. A classic experiment examined competition between rock barnacles (*Semibalanus balanoides*) and little gray barnacles (*Chthamalus stellatus*), which normally live higher on the shore (see Fig. 11.20). Rocks with newly settled juveniles of both species were collected and placed at different heights. The rock barnacles were removed from some of the rocks, while other rocks were not disturbed.

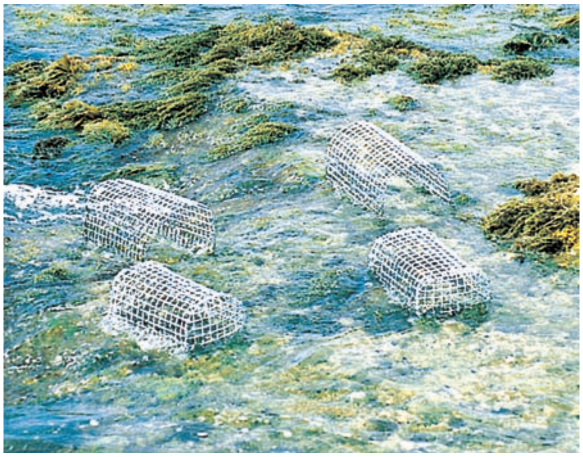
High in the intertidal, little gray barnacles survived better than rock barnacles. They apparently tolerate drying better. Lower in the intertidal, where the rock barnacles can survive, little gray barnacles can't compete. They do quite well as long as the rock barnacles are removed, but when the two species grow together the bigger, faster-growing rock barnacles crush, undercut, or smother the little gray barnacles. Thus, the lower limit of little gray barnacles is determined by a biological factor: competition.

Removal experiments have also shown the importance of grazing and predation. When limpets are removed from test areas, for example, a profusion of seaweeds usually results. While limpets are present the algae cannot establish themselves because limpets scrape young algae off the rocks. If the seaweeds get a foothold, however, they are often able to persist because adult seaweeds can stand up to these grazers. Another removal experiment, involving a sea star, is summarized in Figure 11.22.

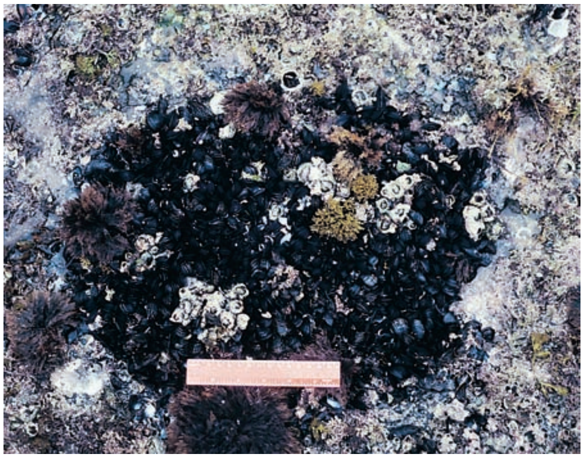
It may be time-consuming, difficult, or downright impossible to remove all the organisms of interest from an area, or they may move back into an area too soon after removal. Instead, **caging experiments** can be used to keep them out. On the Channel Islands off the coast of Southern California, the intertidal is covered by a nearly unbroken carpet of seaweeds. When marine biologists discovered that large numbers of spiny lobsters (*Panulirus interruptus*) moved into the intertidal during nighttime high tides, they wondered what effect the lobsters were having. They installed plastic cages to keep the lobsters out. Just to make sure that the seaweed wasn't affected by the shade of the cages, they also installed control cages that had roofs but no ends, allowing lobsters to enter unimpeded. Seaweeds continued to flourish in these control areas and in adjacent open areas, but within the fully enclosed cages the seaweeds were soon replaced by mussels. This demonstrated that seaweeds were able to dominate because the lobsters ate the mussels, which are superior competitors.

Caging experiments don't have to use actual cages, just some sort of barrier to keep the animals out. Plastic rings or strips of artificial turf, for example, will keep out sea stars, limpets, and snails, which can't crawl over the turf. Cages can also be used to hold animals inside an area, rather than keep them out, to determine their effects.

Transplantation, removal, and caging experiments have been extraordinarily effective in unraveling the web of physical and biological interactions in the intertidal zone—so effective, in fact, that they have become an important tool for ecologists not only in the intertidal but in many other environments.



These cages were used in California to test the effects of spiny lobsters (*Panulirus interruptus*) in the intertidal zone. The lower cages have closed ends to keep lobsters out. The upper cages have open ends to allow lobsters free access and are controls for the effects of the cages themselves.



The mussels in this dark patch have taken over the space inside a closed cage, which was removed for the photo. The surrounding rock is dominated by red algae, as are areas inside open-ended cages, not visible in this photo. The conclusion of the experiment is that mussels would dominate the community if not eaten by lobsters.

the tides on a regular basis. A **diurnal tide** exposes the organisms once a day, a **semidiurnal tide** twice. If the tide is **mixed,** the lower of the two successive high tides may not submerge the high part of the zone, and the higher of the two lows may not expose the bottom part. Thus, even in places with a semidiurnal tide, parts of the middle intertidal zone may be submerged or exposed only once a day. With so much variation in emersion time, different heights within the middle intertidal often support different organisms. In other words, the middle intertidal is often made up of several separate vertical zones.

The upper boundary of the middle intertidal is almost always marked by a band of acorn barnacles. In many places at least two species of barnacles, such as little gray (*Chthamalus*) and rock barnacles (*Balanus, Semibalanus*), form distinct bands, with little gray barnacles living higher up.

Experiments (see "Transplantation, Removal, and Caging Experiments," p. 252) show that this zonation results from a combination of the barnacles' larval settlement pattern, desiccation tolerance, competition, and predation (Fig. 11.20). The larvae of both species settle over a wider range than is occupied by adults. The upper limit of both species appears to result from emersion, because larvae that settle too high in the intertidal die. Little gray barnacles tolerate drying better than rock barnacles and can therefore live higher up. At lower levels, where the rock barnacles can survive, they outcompete the little gray barnacles. Adult little gray barnacles, then, live perched in a narrow band above their competitors where they can survive emersion.

The lower limit of rock barnacles, like that of little gray barnacles, is determined by biological factors, in this case both predation and competition. Whelks are major predators of barnacles (Fig. 11.21). These snails use their radula to drill holes in barnacles' shells. They also secrete chemicals that soften the shells. If protected from the snails by wire cages, rock barnacles flourish below their normal limit. Unprotected barnacles, however, suffer heavy losses to snail predation. The only thing that saves the rock barnacles is that the dog whelks do most of their feeding during high tide. When emersed they lose a lot of water if they move around hunting barnacles, so to avoid desiccation at low tide they cease feeding or move lower in the intertidal. In the upper intertidal, the snails don't have enough time at high tide to eat the barnacles. Sea stars, which also eat barnacles, have the same problem as the snails. Rock barnacles may also face competition from mussels. In some places, in fact, the lower limit of barnacles is set not by dog whelk

Semidiurnal Tide A tidal pattern with two high and two low tides each day.

- Chapter 3, p. 61; Figure 3.34

Diurnal Tide A tidal pattern with one high and one low tide each day.

Mixed Tide A tidal pattern in which two successive high tides are of different heights.

- Chapter 3, p. 61; Figure 3.34

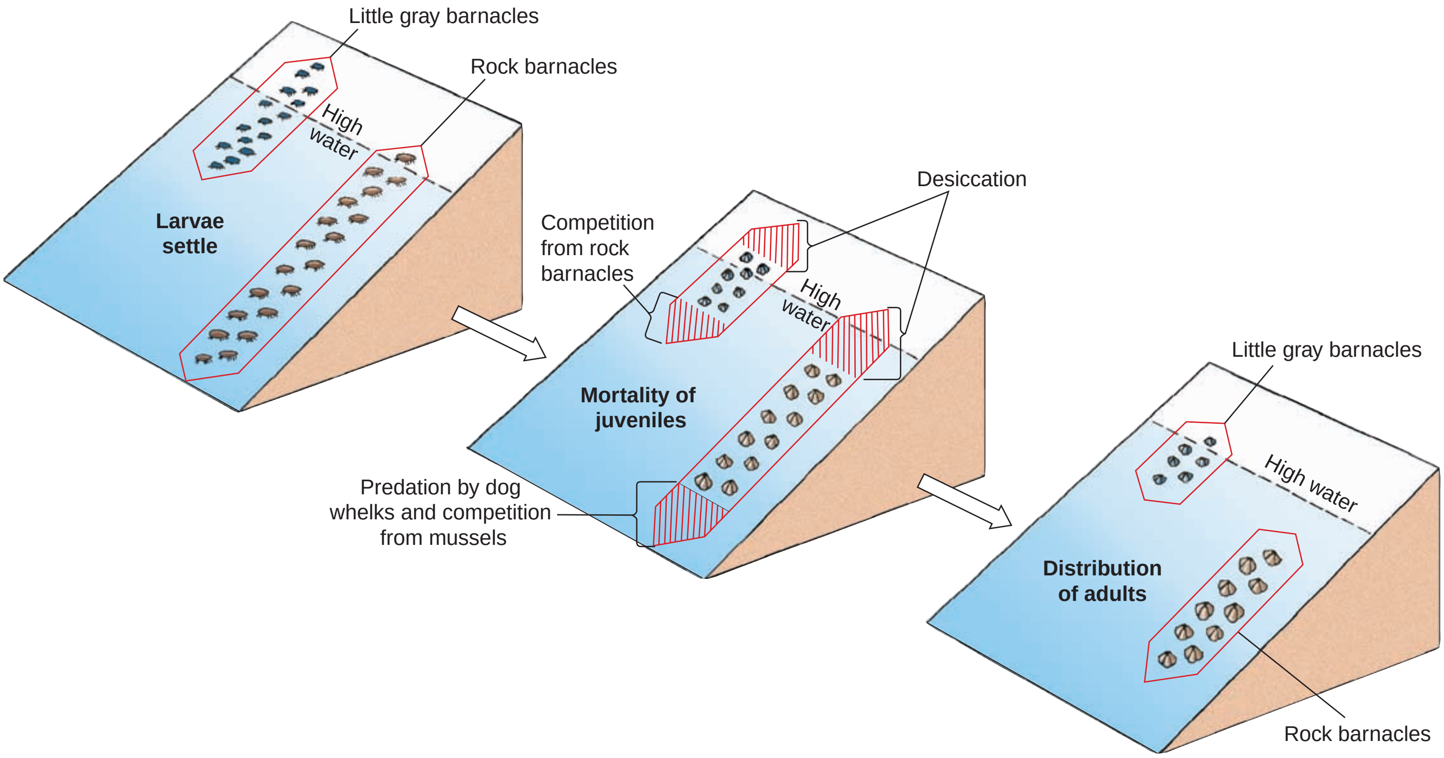


FIGURE 11.20 Larvae of both little gray barnacles (*Chthamalus stellatus*) and rock barnacles (*Semibalanus balanoides*) settle out of the plankton over a wider range of the intertidal zone than is occupied by adults. At the upper edge, young barnacles dry out and die. Little gray barnacles are more resistant so they can live higher on the shore. Little gray barnacles that settle where the rock barnacles can survive, however, are outcompeted. The lower edge of the rock barnacle zone occurs where predatory snails, called dog whelks (*Nucella lapillus*), can easily reach them. In some places, competition from mussels also helps determine the lower limit.

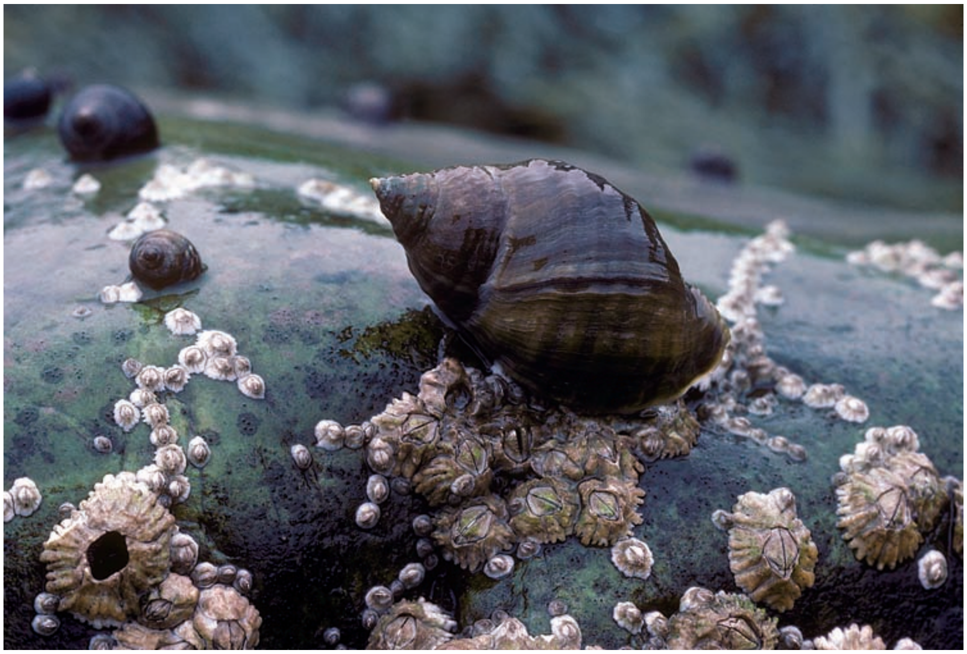


FIGURE 11.21 A dog whelk (*Nucella lapillus*) preying on rock barnacles (*Semibalanus balanoides*) on a rocky shore in Maine. In moist conditions like these the whelk is able to feed at low tide, but it will cease activity if the rock dries out.

predation but by competition with mussels. Like the little gray barnacles, the rock barnacles persist in a narrow zone between the level where they desiccate and die and the level where their enemies can reach them.

Acorn barnacles usually occupy the top of the middle intertidal zone. Their upper limit is determined by how high they can live without drying out. Their lower limit is set by competition with other barnacles or mussels or by snail or sea star predators.

Many other organisms live in the middle intertidal among or below the barnacles. Which organisms are present, how many there are, and where they occur all depend on the unique combination of physical and biological factors at that site. The pattern of the tides, steepness of the shore, exposure to waves, and local weather all have an influence. Predation, competition, and larval settlement patterns are almost always involved. Considering all the possible ways in which these factors might interact gives you some idea of how complicated the story can be.

Depending on all these factors, mussels (*Mytilus*), gooseneck barnacles (*Pollicipes*), and brown seaweeds, particularly rockweeds (*Fucus, Pelvetia*), often dominate the middle intertidal below the barnacles. Many rockweeds have air bladders called **pneumatocysts** that float their fronds closer to the light. They may form a luxuriant thicket, or **algal turf,** that shelters many small animals. Mussels are especially common on stormy, exposed shores. They cannot live as high on the shore as barnacles, because they dry out and also because at high levels they do not spend enough time underwater to filter feed. At levels where they *can* live, however, mussels are dominant competitors, smothering or crowding out other organisms.

Sea stars (*Pisaster, Asterias*) are voracious predators of mussels. Contrary to popular belief, sea stars do not force open a mussel's shell to eat it. Instead, they insert their stomach into the shell and begin digesting the mussel from the inside. Sea stars need only a tiny crack to insert their stomach—only 0.2 mm (0.008 in) for the ochre sea star (*Pisaster ochraceus*). The shell opens after the mussel is weakened.

Sea stars don't tolerate desiccation very well and need to be underwater to search for food (see the photo on p. 241), though they may finish a meal after the tide goes out. In the lower part of the middle intertidal this is no problem, and sea stars take a heavy toll on mussels. Thus, mussels are only found above the level of heavy sea star predation. As with other intertidal species, the lower limit of mussels is set by a biological factor: predation by sea stars.

Mussels are the dominant competitors for space on many rocky shores. Their upper limit is set by desiccation and filter feeding time, their lower limit by predatory sea stars.

In some places spiny lobsters (*Panulirus*) instead of sea stars are the main predators of mussels. The lobsters can almost eliminate mussels from the intertidal zone altogether.

Sea stars and other mussel predators can have a strong effect even above the level where they completely wipe out the mussels. They venture into the mussel bed during high tide and eat some of the mussels before retreating with the tide. This opens up space for other organisms—such as acorn barnacles, gooseneck barnacles, and seaweeds—that would otherwise be crowded out. The sea stars also eat dog whelks, doing the barnacles another favor. If the barnacles live long enough, they get too big for the dog whelks to eat. By reducing the number of dog whelks, the sea stars give the barnacles more of a chance to grow big before a whelk eats them.

The sea stars are absent from areas with extremely strong wave action. In such areas, or if the predators are experimentally removed (Fig. 11.22), mussels take over. They outcompete and crowd out other sessile organisms. Thus, many species can live in the middle intertidal only if sea stars keep mussel numbers under control.

Note that many intertidal species are more abundant than the sea stars, but the sea stars profoundly affect the entire community. This demonstrates a common feature of biological

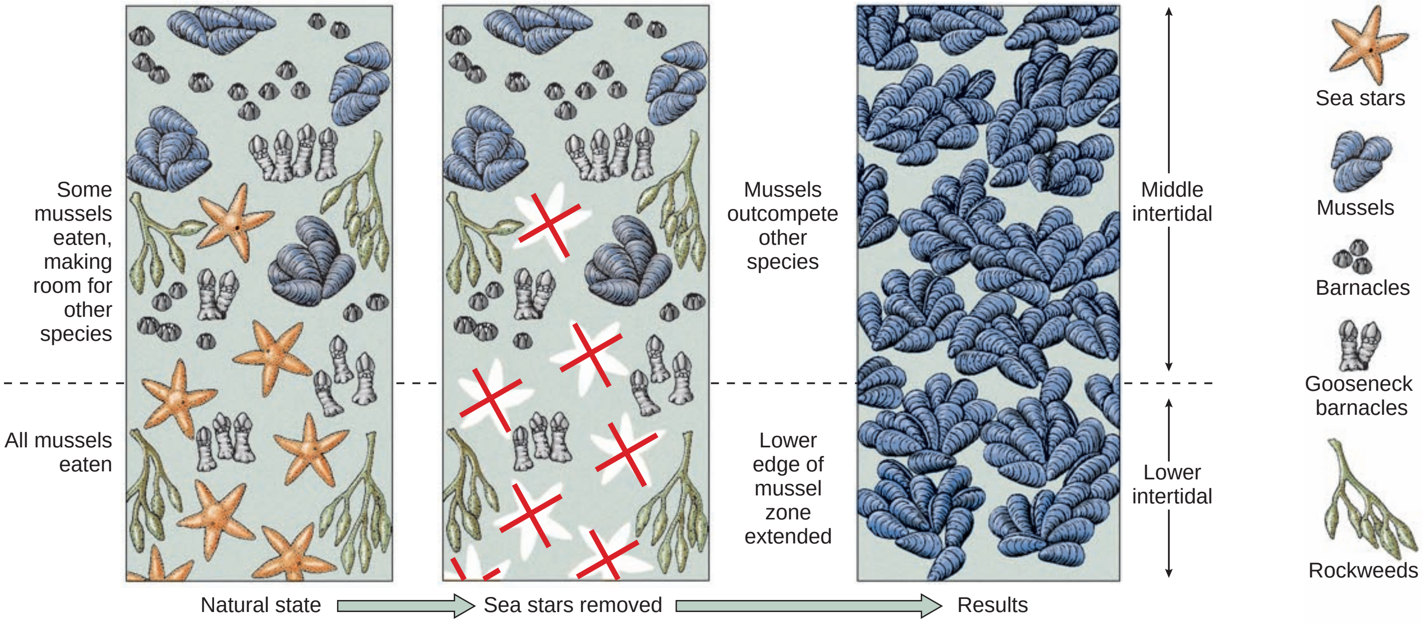


FIGURE 11.22 Removing predatory sea stars—or keeping them out with cages—shows how they affect the middle intertidal community. Below a certain level the sea stars can easily reach the mussels, their favorite food, and eat them all. Above this level the sea stars cannot eat all the mussels, but they eat enough to make space available for other species. When there are no sea stars around, the mussels are able to live lower, and they monopolize the available space by overgrowing and crowding out other species. Sea stars thus maintain the diversity of the middle intertidal community.

communities: Just because a species is relatively uncommon does not mean it is unimportant. Predators whose effects on their communities are proportionately much greater than their abundance are known as **keystone predators.**

Natural disturbances can have effects similar to those of predation. When mussel beds get too dense, clumps of mussels can be torn away by waves (see Fig. 11.14), exposing the bare rock. Drifting logs that batter the rocks and, in cold places, scouring ice and severe freezes, have the same effect of opening up new space. This prevents mussels from monopolizing the available space, allowing other organisms to persist.

When a patch of space is cleared, new organisms often move into the patch and get replaced by others in a regular sequence (Fig. 11.23). The term **ecological succession** is used to refer to such regular patterns of regrowth. In the rocky intertidal the first stage is usually a thin film of bacteria and microscopic algae, such as diatoms, that covers the rock. This film may condition the rock surface, since the settling larvae of some species prefer surfaces with the film over bare rock. Seaweeds often move in next, followed by barnacles and finally mussels, the dominant competitor. The final stage in an ecological succession is called the **climax community.**

The typical steps of ecological succession in the middle intertidal of many rocky shores are, first, a bacterial and algal film, then seaweeds, barnacles, and finally the climax mussel community.

The actual pattern of succession may deviate from the "typical" pattern for many reasons. Grazers like limpets and chitons may remove newly settled larvae and spores. If grazers move into a patch early on, the succession may never get past the bacterial and algal film stage and in some places grazers limit even the film. Predators and other disturbances help determine whether the final stage is a solid mussel bed or a mixture of species.

Furthermore, steps in the succession may be skipped. For example, seaweeds may never be able to colonize a patch if barnacle larvae get there first (see Fig. 11.16). The time of year that the patch is created is important. If the patch opens when barnacle larvae are abundant and seaweed spores are rare, barnacles have the upper hand. There is thus an element of chance in the development of the community. Stages may also be skipped if the bare patch is small. A small patch cleared in the middle of a mussel bed may be taken over by other mussels that move in from the sides before the succession gets started.

Without predation and other disturbances, the best competitors take over and many species disappear from the area. Disturbance can prevent this. Mussels, for instance, are often unable to completely cover middle intertidal rocks because sea stars eat them or waves tear them away. This gives other species a chance. Disturbance can thus increase the number of species that live in an area, that is, the **diversity,** by interfering with **competitive exclusion.** The rocky intertidal in some

Competitive Exclusion The elimination of one species by another as a result of competition.
- Chapter 10, p. 214

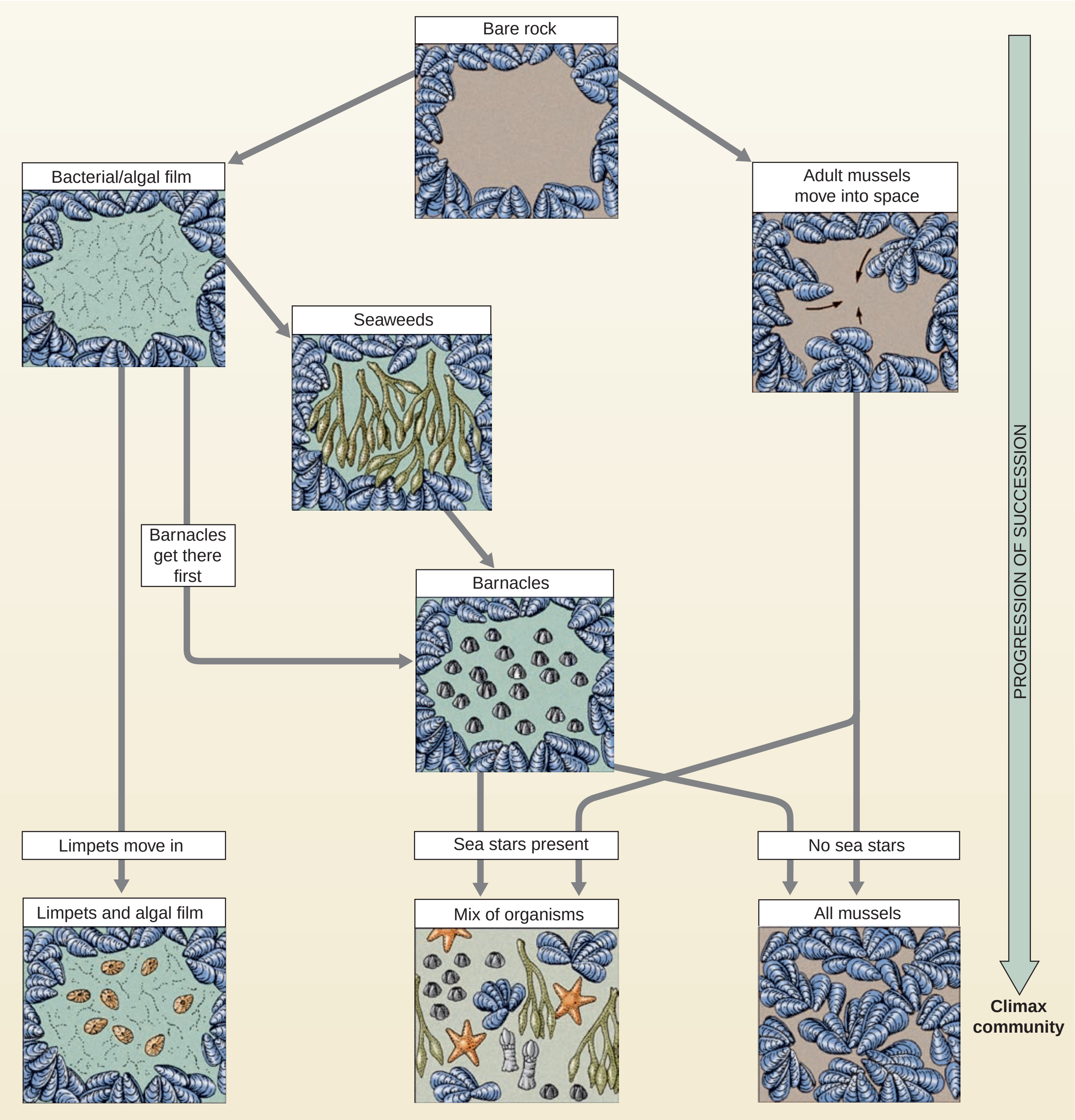

Bare rock
Bacterial/algal film
Adult mussels move into space
Seaweeds
Barnacles get there first
Barnacles
Limpets move in
Sea stars present
No sea stars
Limpets and algal film
Mix of organisms
All mussels
PROGRESSION OF SUCCESSION
Climax community

FIGURE 11.23 Ecological succession following the clearing of a patch in a mussel bed. The pathway taken and the end result depend on the size of the patch, when it opens up, and just plain luck—which organisms get there first.

places can be thought of as a mosaic of patches that were cleared at different times and are in different stages of succession. Each patch supports a different set of organisms, so the number of species in the area as a whole increases. On the other hand, if predation and other disturbances happen too often, the community keeps getting knocked back to the starting point. It never gets a chance to develop, and not many species are able to live there. The highest diversity occurs when there is enough disturbance to prevent the dominant competitors from taking over, but not so much that the community is unable to develop (Fig. 11.24).

In the absence of disturbance a few dominant competitors, especially mussels, take over the space in the middle intertidal zone. Moderate predation and other disturbance prevents this and allows other species to live there. Too much disturbance, however, removes most species.

The Lower Intertidal The lower intertidal is immersed most of the time. This makes it easy for predators like sea stars and dog whelks to feed, so mussels and barnacles are rare. The lower intertidal is dominated by seaweeds, which form a thick turf on the rocks. These seaweeds, including species of red, green, and brown algae, can't tolerate drying out but in the lower intertidal they grow in profusion. Not surprisingly, grazing and competition are important in the lower intertidal. Light, as well as space, is an important resource. Seaweeds often compete by overgrowing each other, blocking the light.

The lower intertidal is dominated by red, green, and brown seaweeds.

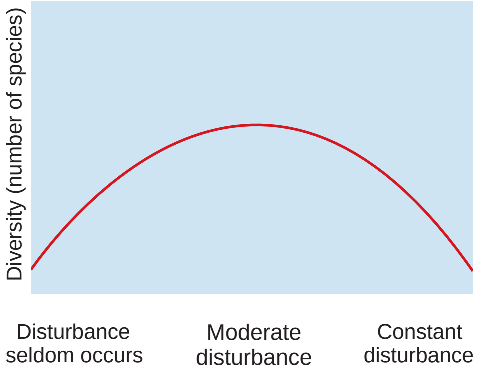


FIGURE 11.24 Other things being equal, the number of species depends on how often disturbances occur. In this context, predation on the dominant competitors counts as a disturbance. When disturbance is rare, the dominant competitors take over and exclude other species. Intermediate levels of disturbance prevent this and give other species a chance. Thus, the number of species is highest when disturbance is moderate. If disturbance happens too often, most species cannot get a foothold and the number of species drops.

A good example of the interaction of competition and grazing comes from the coast of New England. Two common seaweeds there are a green alga, *Enteromorpha,* and a red alga (not actually a moss) called Irish moss (*Chondrus crispus*). When the two seaweeds grow together in tide pools, *Enteromorpha* dominates by overgrowing the Irish moss (Fig. 11.25). Surprisingly, however, Irish moss is the most common seaweed in many tide pools.

The reason for this is that grazing sometimes prevents *Enteromorpha* from taking over. An abundant grazer in the area is the common periwinkle (*Littorina littorea*), which is closely related to the periwinkles that live in the upper intertidal. Although *Enteromorpha* is one of its favorite foods, the snail hardly touches Irish moss. If a tide pool has a lot of snails, they eat the *Enteromorpha* and make way for Irish moss. If snails are transplanted into an *Enteromorpha* pool, *Enteromorpha* quickly disappears and Irish moss takes over. On the other hand, *Enteromorpha* soon moves in after periwinkles are removed from an Irish moss pool.

The story doesn't end there. If the periwinkles like *Enteromorpha* so much you'd think that they would move into *Enteromorpha* pools, but they don't. For one thing, large periwinkles do not move around a lot and prefer to stay in one tide pool. Young periwinkles are eaten by green crabs (*Carcinus maenas*), which also live in tide pools. The crabs, in turn, are eaten by gulls (*Larus*). *Enteromorpha* provides cover for the crabs, protecting them from gulls. The crabs then eat young periwinkles, preventing *them* from colonizing the pool. In Irish moss pools, on the other hand, the crabs lack cover and are eaten by gulls. Without the crabs, young periwinkles can survive in the tide pools. Thus, both types of tide pool community perpetuate themselves as a result of both positive and negative interactions among species.

The lower intertidal supports many other seaweeds besides *Enteromorpha* and Irish moss. These range from delicate reds and greens to large, tough kelps (*Egregia, Laminaria;* see Fig. 13.20). The kelps mark the lower limit of the intertidal and continue down into the **subtidal zone.** There is no precise boundary between the lower reaches of the intertidal and the upper edge of the subtidal. **Coralline algae** (*Corallina, Lithothamnion*) can also be abundant. Surf grass (*Phyllospadix*), a flowering plant, is common in the lower intertidal on the Pacific coast of North America (see Fig. 6.13*e*).

Subtidal Zone The part of the continental shelf that is never exposed by low tide.

- Chapter 10, p. 220; Figure 10.12

Coralline Algae Red algae that deposit calcium carbonate ($CaCO_3$) in their tissues.

- Chapter 6, p. 107; Figure 6.10

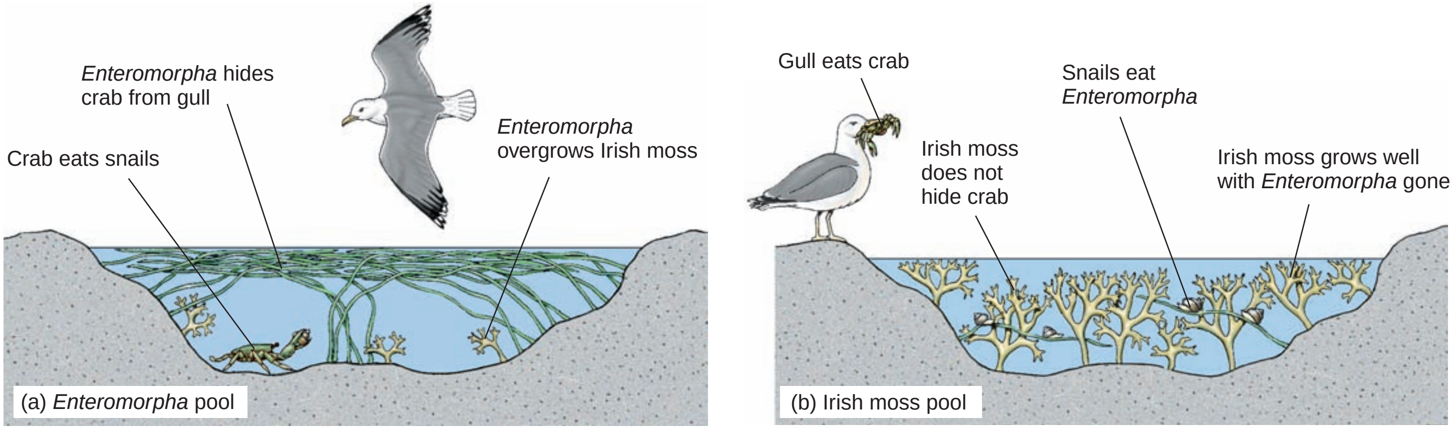

Enteromorpha hides crab from gull
Crab eats snails
Enteromorpha overgrows Irish moss
(a) *Enteromorpha* pool
Gull eats crab
Irish moss does not hide crab
Snails eat *Enteromorpha*
Irish moss grows well with *Enteromorpha* gone
(b) Irish moss pool

FIGURE 11.25 Biological interactions determine what type of seaweed predominates in New England tide pools. Unless something interferes, both types of pool are self-sustaining.

EYE ON SCIENCE

PISCO Studies of Ecological Interactions

To understand intertidal ecosystems we need to consider different scales. Intensive, localized studies are needed to dissect out the detail of how individual organisms interact, while studies of an entire bay or a coastline provide a broader perspective. Examining links between the intertidal and coastal ecosystems offshore provides an even bigger picture. Time scale is critical, too: A one- or two-year study can't detect long-term changes in a community, and what seems like a major shift can just be natural variation. Similarly, while studies of single factors, sea star predation for example (see Fig. 11.22), reveal much about intertidal ecology, we also need to understand how different factors interact—for example, how sea star predation, mussel and algal growth rates, and larval settlement might affect competition between mussels and seaweeds.

Studies that combine large spatial and temporal scales and multiple factors require time, expertise, and funding that are usually beyond the reach of individual investigators or research teams, so marine ecologists are increasingly joining forces. The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) is a consortium of marine scientists doing integrated studies at many sites over many years along 2,000 km (1,250 mi) of the Pacific coast of the United States. Research on oceanography, molecular biology, genetics, physiology, and ecology provides the most comprehensive view ever of the nearshore ecology of this coastline.

"Robomussel" is an electronic temperature recorder that not only looks but also absorbs heat like real mussels.

In the rocky intertidal, PISCO scientists up and down the coast regularly measure the abundance, growth, and larval settlement rates of major species, study the intensity and effects of predation and competition, and monitor physical factors such as temperature and salinity. All studies use the same sites and are linked to research on the oceanography and biology of adjacent nearshore waters. PISCO research has already revealed that there is much more spatial variation in larval settlement and individual species' distributions than previously thought, and that coastal upwelling (see "Upwelling and Productivity," p. 351) influences predation, grazing, and other processes in the rocky intertidal.

In the summer of 2002 PISCO scientists discovered an unprecedented hypoxic (low-oxygen) "dead zone" near the Oregon coast, which has since recurred every summer, progressively getting larger and lasting longer. Unlike hypoxic zones caused by nutrient overfertilization and decay of the resulting algal growth this one forms when upwelling currents carry water from the naturally occurring oxygen minimum zone (see "The Oxygen Minimum Zone," p. 367) onto the shallow nearshore shelf. Scientists suspect a large-scale change in oceanographic conditions, perhaps related to climate change, but research to understand this phenomenon continues.

To learn how climate change might directly affect intertidal communities, PISCO scientists placed "Robomussels" in mussel beds from Washington to Southern California to determine the effects of splashing waves, tide, and latitude on the mussels' body temperatures. They discovered "hot spots" along the entire coast where mussel temperatures were higher than would be expected based just on how far north they were. It was previously assumed that the impacts of global warming will mainly occur on the edges of species' ranges, as the southern end gets too hot and the northern end warms up, but this research indicates that mussels could die off in patches all along the coast, likely affecting the entire community.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

A host of small animals live among the seaweeds, hiding from predators and staying moist during very low tides. Sea urchins (*Strongylocentrotus, Echinometra;* see Fig. 13.19) are common grazers on the seaweeds. Also present in the lower intertidal are sea anemones (*Metridium, Anthopleura;* Fig. 11.26), polychaete worms (*Spirorbis, Phragmatopoma*), snails (*Tegula, Nucella*), sea slugs (*Aplysia, Dendronotus*), and many others.

Most rocky intertidal fishes live in the lower intertidal or in tide pools. Gobies, clingfishes, sculpins (*Oligocottus*), pricklebacks (*Cebidichthys*), and gunnels (*Xererpes*) are among the most common.

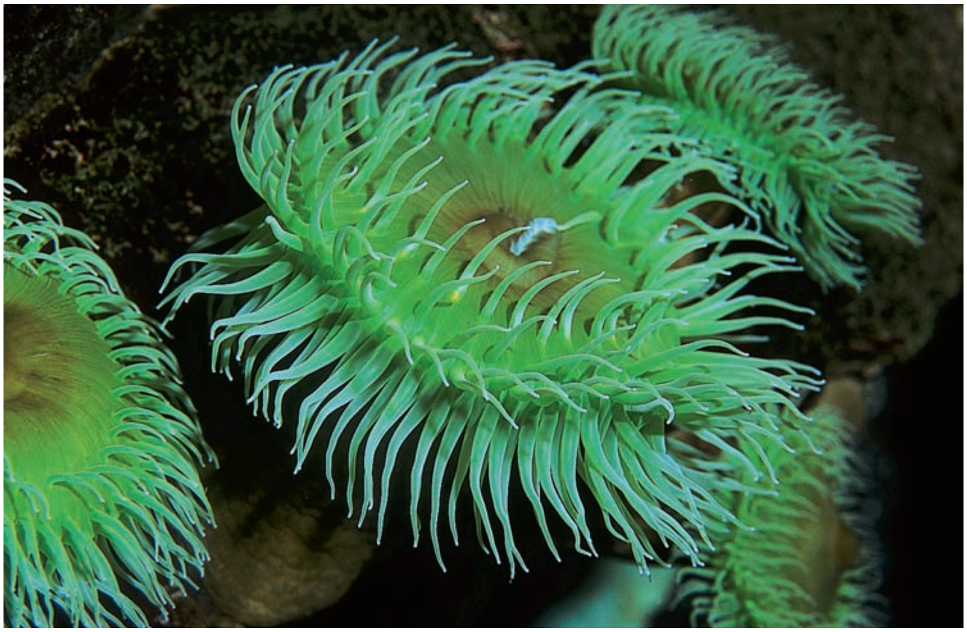


FIGURE 11.26 The giant green sea anemone (*Anthopleura xanthogrammica*) from the Pacific coast of North America catches small prey with its tentacles but also gets nutrition from zooxanthellae, symbiotic algae in its tissues.

These are all small fishes adapted to the environmental extremes of the intertidal. Most are carnivorous.

SOFT-BOTTOM INTERTIDAL COMMUNITIES

Any bottom that is composed of sediment, as opposed to rock, is considered a **soft bottom.** The dividing line isn't always clear. Boulder fields are usually thought of as rocky, but how small the rocks have to be before the bottom is considered soft is not precisely defined. In this text we refer to a bottom as soft if organisms are able to burrow in it easily.

Soft bottoms occur where sediments accumulate. In North America, soft bottoms dominate on the east coast south of Cape Cod and virtually all of the Gulf coast (see foldout map). The rocky west coast is often interrupted by sandy beaches and mudflats, especially in and near river mouths. Whether and what kind of sediment accumulates in an area depends on how much water motion there is and on the source of the sediment. In turn, the type of sediment strongly influences the community.

The Shifting Sediments

Soft bottoms are unstable and constantly shift in response to waves, tides, and currents. Thus, soft-bottom organisms do not have a solid place for attachment. Very few seaweeds have adapted to this environment. Seagrasses are the most common large primary producers on soft bottoms and often form dense intertidal beds. In this chapter we deal only with intertidal soft-bottom communities that lack seagrasses. Seagrass communities are discussed in Chapter 13 (see "Seagrass Beds," p. 290).

The animals that live on soft bottoms also lack solid attachment sites. Though a few of them are epifauna and live on the sediment surface, most burrow in the sediment for protection and to keep from being washed away. Animals that burrow in the substrate are called **infauna** because they live *in* the sediment.

The kind of sediment on the bottom, especially the size of the grains, is one of the most important physical factors affecting soft-bottom communities. Most people use the terms "sand," "silt," "clay," and "mud" without much thought. To a geologist these terms refer to sediments with specific particle sizes (Fig. 11.27).

Careful analysis is needed to determine grain size precisely, but a "quick and dirty" test will literally give you a feel for the different sediment types. Rub a pinch of sediment or soil between your fingers. Any grittiness is caused by sand. Silt and clay, which together are called mud, feel smooth. Also, the finest sand particles are the smallest you can see. To tell silt and clay apart, you can rub a little between your teeth. Silt feels gritty, but clay is still smooth.

> The terms "sand," "silt," and "clay" refer to sediments of particular grain sizes. Sand is the coarsest, followed by silt and then clay. "Mud" refers to silt and clay together.

Most sediments are made up of a mixture of different particle sizes. They are described according to the most common grain size. Sand, for instance, has mostly sand-sized grains but may also have small amounts of mud or a few large rocks.

Sediment composition is directly related to the degree of water motion. Imagine, or better yet actually perform, the following experiment. Take a handful of sediment or soil that contains

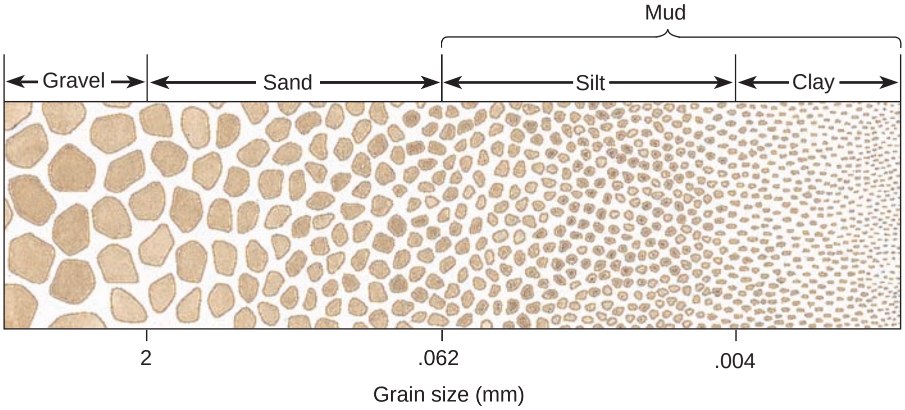


FIGURE 11.27 Sediments are classified by the size of the particles. Sand is relatively coarse; clay is very fine. Together, silt and clay are called mud.

a wide range of particle sizes, from large pebbles down to clay. Put it in a container with some water and shake it up. As soon as you stop shaking, the pebbles will sink to the bottom. As the water gradually stops moving, first the coarse sand and then finer particles will begin to sink. Very fine material will remain suspended for a long time, making the water look muddy. You might have to let the container sit for weeks before the finest clay settles out completely. If the container is stirred even gently, the fine material will never settle out.

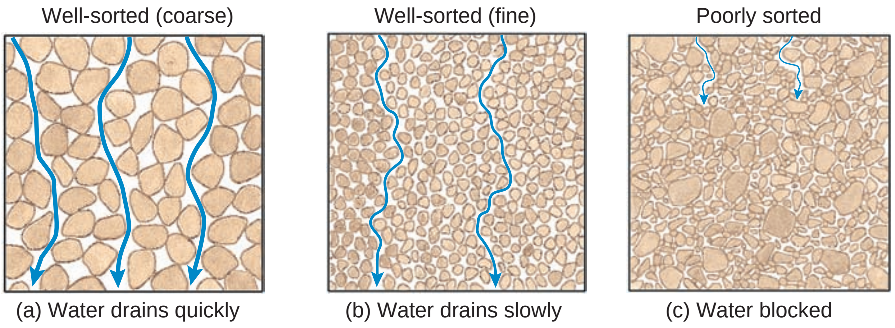


FIGURE 11.28 "Sorting" refers to the uniformity of grain size in the sediment. In well-sorted sediments (*a* and *b*) the grains are all about the same size. There is a lot of space between the grains, so water can flow through. The grain size, as well as sorting, affects how well water circulates; larger grains have larger spaces and are thus more porous. Poorly sorted sediments (*c*) have many different-sized grains. Small grains fill in the spaces between the larger ones, making water flow difficult.

This demonstrates a general rule: Fine sediments remain suspended with even a small amount of water motion, whereas coarse sediments settle out unless there is considerable flow. Bottom sediments thus reflect prevailing conditions. Calm, sheltered areas have muddy bottoms because fine sediments can settle out. Particles of organic matter sink at about the same rate as clay particles, so the two tend to settle out together; clay sediments are therefore organic-rich. Places with stronger waves and currents have coarser bottom sediments. If the water motion is strong enough, it may carry away *all* the loose material, leaving bare rock or large boulders.

Fine sediments are found in calm areas such as bays and lagoons. Coarser sediments are found in areas affected by waves and currents.

In our sediment experiment, all the particles would eventually settle out if the container were kept still. A constant flow of water through the container, however, would carry away the fine material and only certain particles, the coarse ones, would remain. The coarse particles would be sorted out from the fine ones.

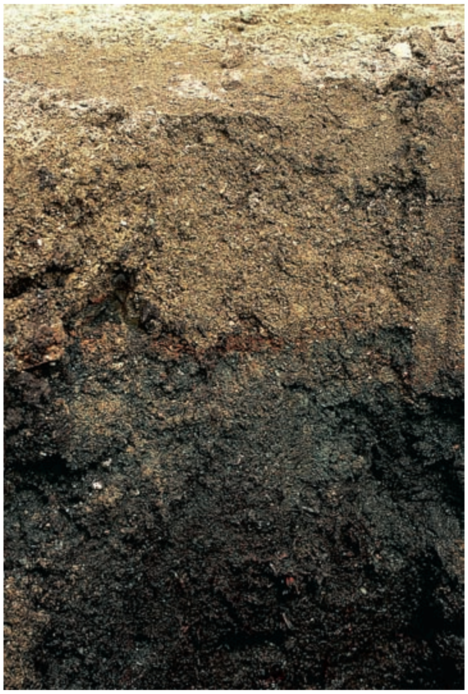


FIGURE 11.29 The black layer in the sediments shows where the oxygen has been completely depleted and hydrogen sulfide (H_2S) is produced by anaerobic bacteria.

Living in the Sediment

Living in sediment has advantages in the intertidal. Soft bottoms stay wet after the tide is out, so the problem of desiccation is not as critical as in the rocky intertidal. This depends on the grain size, however. Coarse sands drain, and therefore dry out, quite rapidly (Fig. 11.28). Partially because of this, coarse sand beaches have relatively little animal life.

Oxygen Availability The amount of organic matter in bottom sediments is particularly important to deposit feeders. Because there are relatively few primary producers, detritus is the main source of food for intertidal soft-bottom communities. Deposit feeders extract this organic matter from the sediments. The amount of detritus depends on grain size (see Fig. 13.12). Coarse sands contain very little organic matter. That is why we tend to think of sand as clean. Silt and clay, on the other hand, are usually rich in detritus, which is why they are often smelly.

The grain size also affects the amount of available oxygen in the sediments. Oxygen in sediments is used up by the **respiration** of animals and, more importantly, decay bacteria. Below the sediment surface there is no light and therefore no photosynthesis, so the infauna depend on the circulation of water through the sediments to replenish the oxygen supply. Grain size and the degree of sorting strongly affect how porous a sediment is (Fig. 11.28). Every backyard gardener knows that water flows more easily through sand than clay. Water circulation through fine sediments is greatly restricted.

Muddy bottoms, then, have a double problem. First, they have more organic material to decay and use up oxygen. Second, the flow of water that brings in new oxygen is reduced. Except for the upper few centimeters of mud the **interstitial water,** or water between the grains, is deficient in oxygen. If you go very far down at all, in fact, the oxygen is completely used up. Sediments with absolutely no oxygen are said to be **anoxic.**

Anoxic conditions are no problem at all for bacteria that are capable of **anaerobic respiration,** in which they break down organic matter without oxygen. A noxious gas called **hydrogen sulfide (H_2S)** is produced as a by-product (see Table 5.1). If you have ever had to unclog the drain of your kitchen sink, you have probably run into hydrogen sulfide. It turns things black and smells like rotten eggs. In the sediments, just as in your drain, hydrogen sulfide is produced when bacteria continue to decompose organic material after all the oxygen has been used up. A distinct black layer appears where anoxic conditions begin in the sediments (Fig. 11.29).

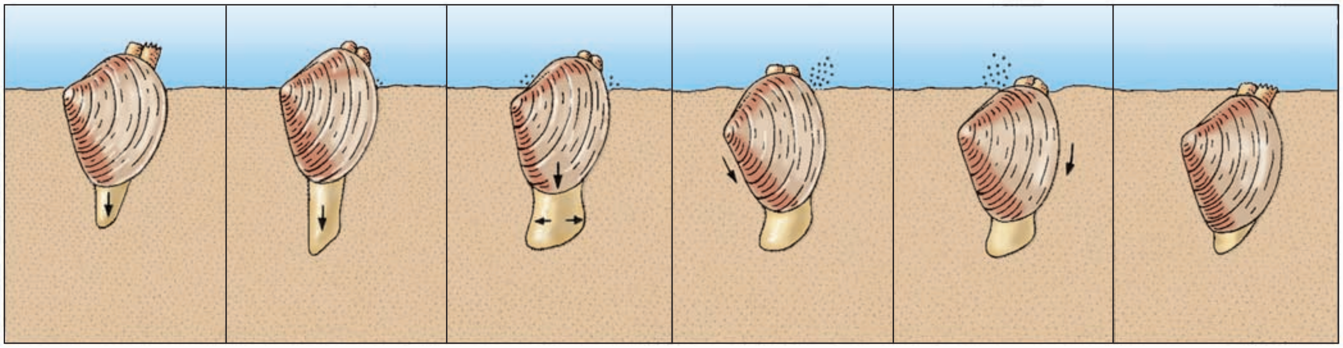


FIGURE 11.30 Burrowing in clams and cockles. The foot does all the work. The clam first pushes its foot down through the sediment. Then the clam expands the end of the foot, which anchors the clam as it pulls its body down.

The decay of organic matter in the sediments uses up oxygen. Because of this, the interstitial water beneath the sediment surface is often depleted of oxygen, especially in fine sediments.

The infauna must adapt to the short supply of oxygen, especially in muddy bottoms. Many animals pump oxygen-rich water from the sediment surface with siphons or through their burrows (see Fig. 12.11). Such animals are never actually exposed to low oxygen levels. Their burrows, and the effects of **bioturbators**—infauna that burrow through, turn over, or otherwise disturb the sediment—help oxygenate the sediment.

Nevertheless, muddy sediments are often oxygen deficient. Animals living in them have adapted to low-oxygen environments. They often have special **hemoglobins** and other adaptations to extract as much as possible of what little oxygen there is in the interstitial water. Some are sluggish, which reduces their oxygen consumption. They may even have a limited capability to carry out anaerobic respiration. A few animals have symbiotic bacteria that help them live in low-oxygen sediments. Even so, hydrogen sulfide is highly toxic, and anoxic sediments have relatively little animal life.

Getting Around Soft-bottom animals use a variety of methods to burrow through the sediments. Clams (*Macoma, Donax*) and cockles (*Cardium*) take advantage of being able to change the shape of their muscular foot. First, they make the foot thin and reach forward with it (Fig. 11.30). Then, the end of the foot thickens and acts as an anchor while they pull the rest of the body along. Many soft-bodied animals do something similar, using their body the way clams use the foot (Fig. 11.31). Some worms force their pharynx into cracks in the sediment to expand the crack before pulling their bodies along behind. Heart urchins (*Lovenia, Echinocardium;* see Fig. 13.7) burrow or plough through the sediment with their spines and tube feet. The many crustaceans that live on soft bottoms—such as amphipods (*Talitrus, Corophium*); sand, or mole, crabs (*Emerita*); and ghost (*Callianassa*) and mud (*Upogebia*) shrimps—use their jointed appendages to dig.

Quite a few deposit feeders solve two problems at once by eating their way through the sediment. Sea cucumbers, certain worms, and other animals use the same inchworm style of locomotion as do the clams and worms described previously, with one important exception. Rather than push through the sediments, they push the sediments *through them.* They digest the organic matter and leave the rest of the sediment behind (Fig. 11.32).

Some soft-bottom animals are so small that instead of burrowing through the sediments they live in the interstitial spaces between the grains. These animals are collectively called the **meiofauna.** There are many different types of animals in the

Respiration
Organic matter + $O_2 \rightarrow CO_2 + H_2O$ + energy
(glucose)
- Chapter 4, p. 67

Hemoglobin Red protein in the blood of vertebrates and some invertebrates that transports oxygen.
- Chapter 8, p. 164

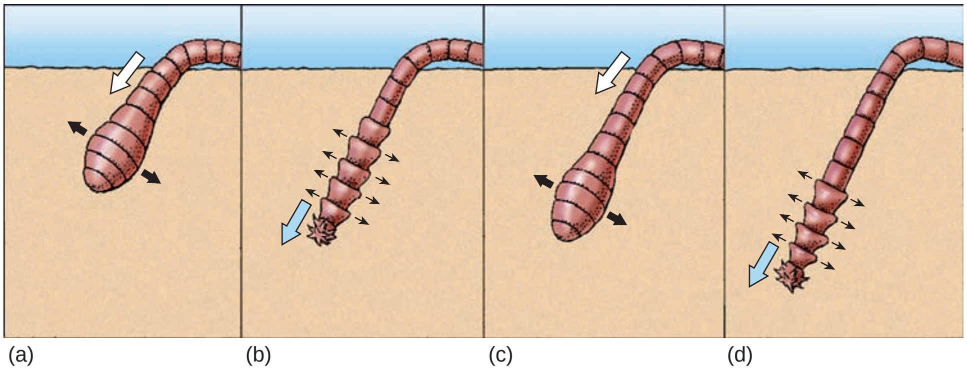


FIGURE 11.31 Burrowing in the lugworm (*Arenicola*). (*a*) The worm expands the end of its body (black arrows). The expanded end acts as an anchor and the rest of the body is pulled along behind (white arrow). (*b*) The worm then flares its segments (black arrows), which prevents it from sliding backward when it pushes its proboscis forward (blue arrow). As the process is repeated (*c* and *d*), the worm moves forward through the sediment.

meiofauna, but most have independently evolved a worm-like shape (see "Life in Mud and Sand," p. 291).

Feeding As already noted, detritus is the main source of food in the soft-bottom intertidal (Fig. 11.33). **Diatoms** sometimes form highly productive mats on the sediment surface, but most of the time they don't account for much primary production. In any case, most animals don't distinguish between the diatoms and detritus. **Plankton** brought in by the tides also make a small contribution to the food supply.

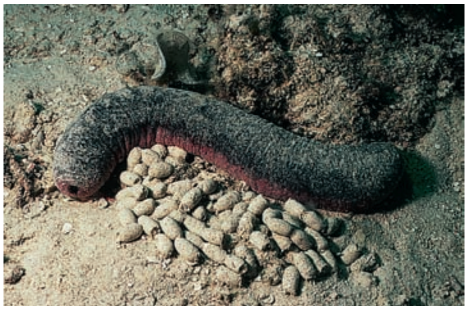


FIGURE 11.32 After digesting out the organic matter, this tropical sea cucumber (*Holothuria edulis*) has deposited a pile of undigested sand pellets.

Many different methods of deposit feeding have evolved. One of the more common methods has already been described: Animals such as sea cucumbers and various worms take in sediment as they burrow, digest the detritus and small organisms, and leave the rest of the sediment in their wake. This technique is more common on mud bottoms than sand, probably because mud contains more organic matter. Sand is also abrasive and hard on the digestive system.

Sand dollars (*Mellita, Dendraster;* see Figs. 7.47 and 13.8) are more selective. They use their tube feet to pick up organic particles. Sand dollars burrow near the sediment surface, where detritus is still accumulating and is therefore more abundant.

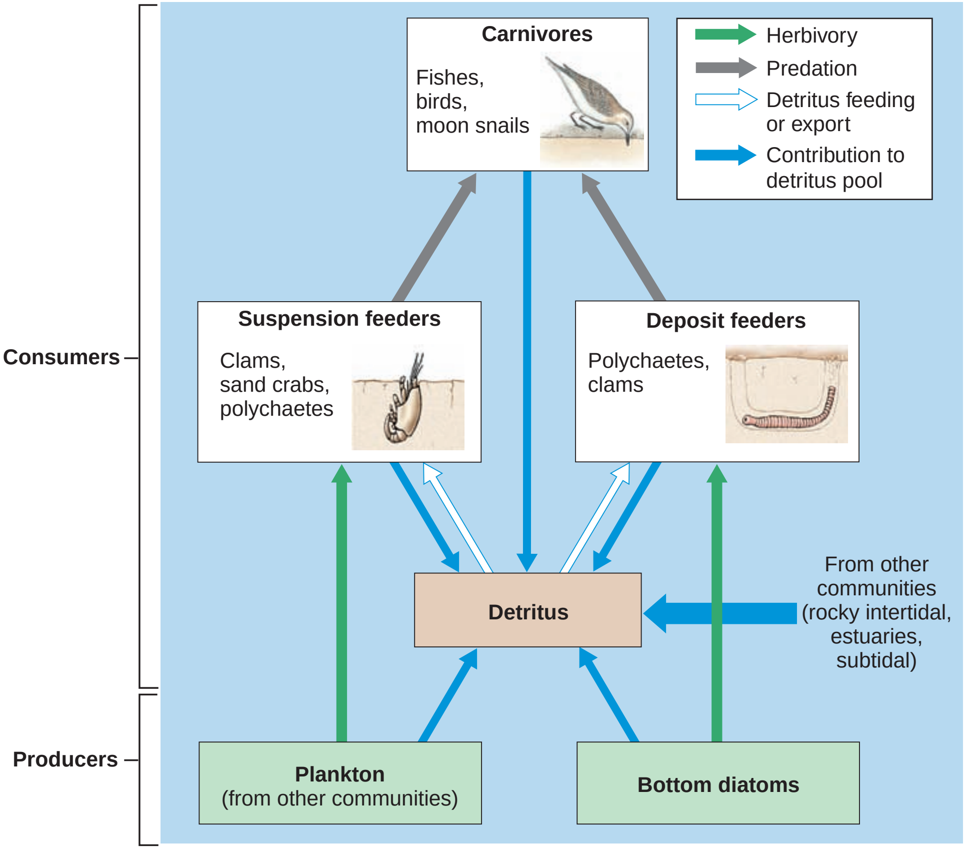

Carnivores
Fishes, birds, moon snails
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Consumers
Suspension feeders
Clams, sand crabs, polychaetes
Deposit feeders
Polychaetes, clams
Detritus
From other communities (rocky intertidal, estuaries, subtidal)
Producers
Plankton (from other communities)
Bottom diatoms

FIGURE 11.33 A generalized food web on a sandy beach.

The bent-nosed clam (*Macoma;* see Fig. 12.11) also concentrates on the upper layer of sediment. It uses a long siphon to suck up food particles from the surface. Other animals catch particles as they settle out and are thus on the line between suspension feeding and deposit feeding. Some polychaete worms (*Terebella*) have long, sticky tentacles that they spread out on the bottom to gather food (see Fig. 13.11). Other polychaetes produce a mucus net that they use instead of tentacles.

There are also suspension feeders, which don't wait for the detritus to settle. An olive shell (*Olivella*) from Central America makes a mucus net, but instead of spreading the net on the bottom the snail holds the net up in the water to filter food. Sand, or mole, crabs hold a pair of large, bushy antennae up into the water to trap food. By quickly burying and uncovering themselves, they combine feeding and locomotion. When the tide is coming in and they want to move up the beach, they uncover just before a wave hits, ride the wave up, and raise their antennae. Then they burrow to keep from being washed back down. As the tide recedes, they do the opposite, burrowing before the wave arrives, then popping out to ride the backwash down the beach.

Soft bottoms also have their share of predators. Moon snails (*Polinices*) burrow through the upper sediments looking for clams. When a snail finds a clam, it drills a hole in the clam's shell and eats it. Several polychaetes and other worms are also important predators. Birds can be major predators during low tide (see Fig. 12.12). At high tide, fishes can come in. Fishes often don't eat an entire animal. Instead, they just nip off clam siphons or other bits that stick out.

Zonation Because the organisms live in the sediments and can't be seen, zonation on intertidal soft bottoms is not as obvious as in the rocky intertidal. Zonation does exist, however, especially on sandy beaches (Fig. 11.34). Water drains rapidly from the sand, and because the beach slopes, the upper part is drier than the lower part.

The upper beach is inhabited by beach hoppers, or sand fleas, which are really amphipods, and by isopods. In warmer areas, these small crustaceans are replaced by ghost (*Ocypode*) and fiddler crabs (*Uca;* see "Fiddler on the Mud," p. 273) that scurry about catching smaller animals, scavenging bits of dead meat,

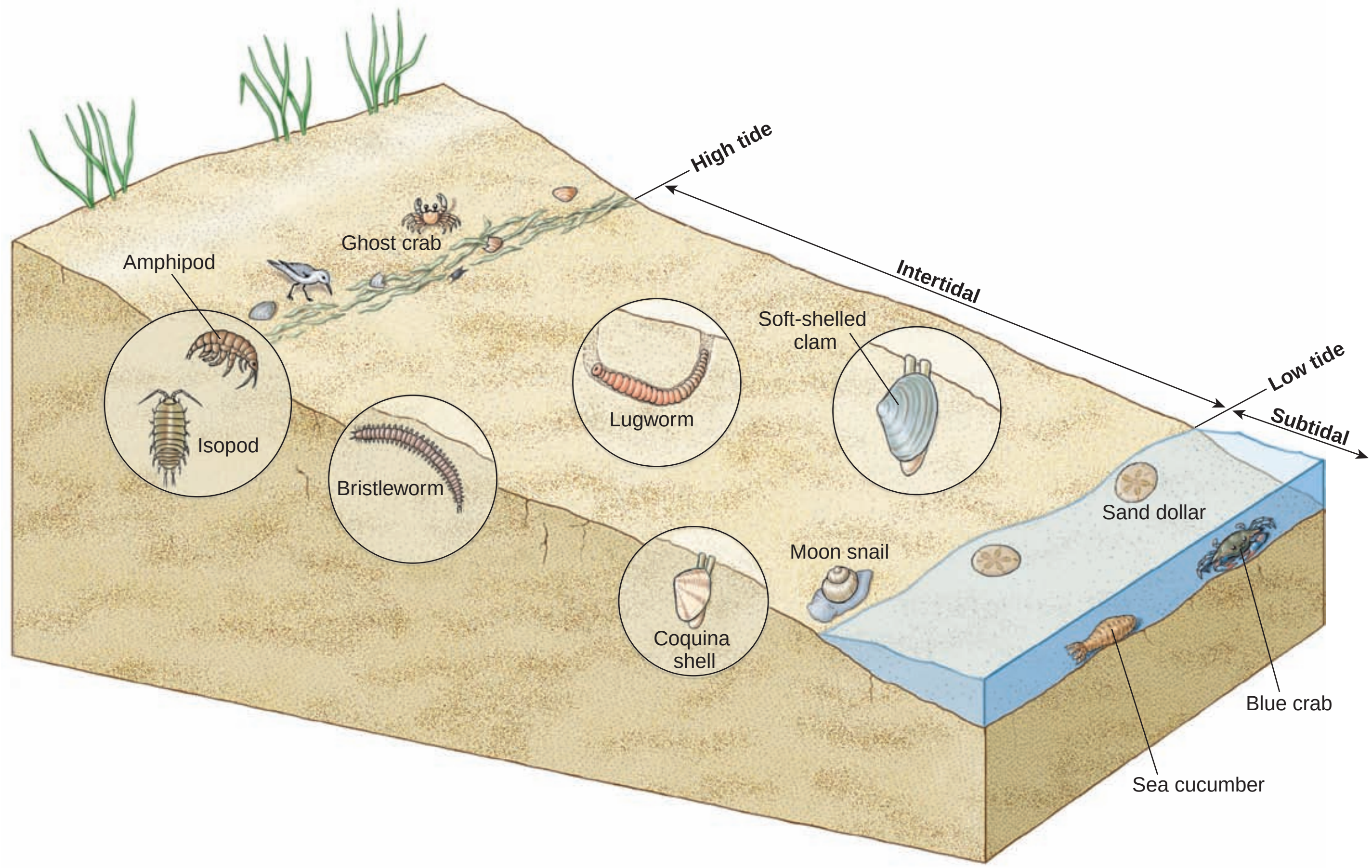

High tide
Intertidal
Low tide
Subtidal
Ghost crab
Amphipod
Isopod
Bristleworm
Lugworm
Soft-shelled clam
Coquina shell
Moon snail
Sand dollar
Blue crab
Sea cucumber

FIGURE 11.34 Generalized zonation pattern on sandy beaches of the Atlantic coast of North America. Sheltered and exposed beaches have different communities, and the animals shown here don't usually all occur on the same beach.

and gathering detritus. Polychaetes, clams, and other animals appear lower on the beach.

Zonation is even less obvious in muddy areas. The bottom in such places is flat, and fine sediments retain water. The habitat therefore does not change very markedly between the high- and low-water marks, and intertidal communities on muddy bottoms are much like the subtidal ones described in Chapters 12 and 13.

Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

- Chapter 10, p. 220; Figure 10.11

Diatoms Single-celled algae with a shell, or test, made of silica.

- Chapter 5, p. 94; Figure 5.6

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. There are marked differences in the type of organisms found at four different locations at the same tidal height along a rocky shore. What might account for this? Offer at least three possible explanations.
2. Most marine biologists hypothesize that space, not food, limits populations in the rocky intertidal. What kind of experiments could be performed to test this hypothesis?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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In Depth

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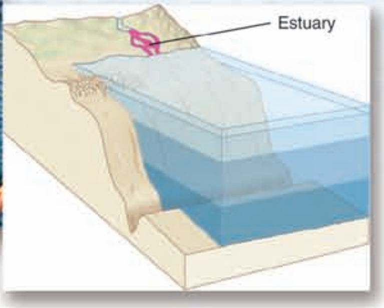
Salt marsh and mudflat.

CHAPTER 12

Estuaries: Where Rivers Meet the Sea



A unique environment develops where fresh water from rivers enters the sea. **Estuaries** are semi-enclosed areas where fresh water and seawater meet and mix. They therefore represent a close interaction between land and sea. Estuaries are typically inhabited by fewer species than rocky shores. Nevertheless, they are among the most productive environments on earth.

Estuaries also rank among the environments most affected by humans (see “Human Impact on Estuarine Communities,” p. 281). Most natural harbors are estuaries, and many of the world’s great cities—New York, London, and Tokyo among others—developed along them. And this was just the beginning.

ORIGINS AND TYPES OF ESTUARIES

Estuaries are scattered along the shores of all the oceans and vary widely in origin, type, and size. They may be called lagoons, sloughs, or even bays, but all share the mixing of fresh water with the sea in a partially enclosed section of the coast. Some oceanographers go as far as classifying enclosed seas with restricted circulation, such as the Baltic and Black seas, as estuaries.

Estuaries are partially enclosed coastal regions where fresh water from rivers meets and mixes with seawater.

Many estuaries were formed when sea level rose because of the melting of ice at the end of the last ice age, about 18,000 years ago. The sea invaded lowlands and river mouths in the process. These estuaries are called **drowned river valleys** or **coastal plain estuaries.** They are the most common type of estuary. Examples are Chesapeake Bay and the mouth of the Delaware River on the east coast of the United States (Fig. 12.1). Other examples are the mouth of the St. Lawrence River in eastern Canada and the mouth of the River Thames in England.

A second type of estuary is the **bar-built estuary.** Here the accumulation of sediments along the coast builds up **sand bars** and **barrier islands** (see "Sand on the Run, or What to Do with Our Shrinking Beaches," p. 418) that act as a wall between the ocean and fresh water from rivers. Bar-built estuaries are found, for instance, along the Texas coast of the Gulf of Mexico, the section of the North Carolina coast protected by the Outer Banks and Hatteras barrier islands (Fig. 12.1), and along the North Sea coast of the Netherlands and Germany.

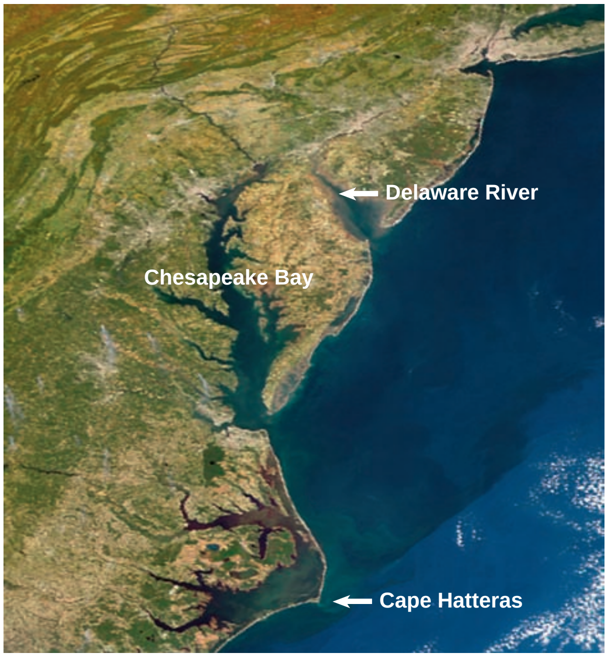


FIGURE 12.1 Two types of estuaries are found along the eastern coast of the United States. Chesapeake Bay and the mouth of the Delaware River are drowned river valley estuaries; the Cape Hatteras islands form a bar-built estuary.

Other estuaries, such as San Francisco Bay in California, were created not because sea level rose but because the land sank, or **subsided,** as the result of movements of the crust. These are known as **tectonic estuaries.**

Another type of estuary was created when retreating glaciers cut deep, often spectacular, valleys along the coast. The valleys were partially submerged when sea level rose, and rivers now flow into them. These estuaries, or **fjords,** are common in southeastern Alaska, British Columbia, Norway, southwestern Chile, and the South Island of New Zealand (Fig. 12.2).

> Estuaries can be classified into four basic groups based on their origins: drowned river valleys, bar-built, tectonic, and glacier-carved estuaries, or fjords.

Broad, well-developed estuaries are particularly common in regions with flat coastal plains and wide continental shelves, a feature typical of **passive margins.** This is the case along the Atlantic coast of North America. The opposite is true for the steep coasts and narrow continental shelves of the Pacific coast of North America and other **active margins.** Here narrow river mouths carved along the steep coast have restricted the formation of estuaries.

FIGURE 12.2 Milford Sound, on the southwestern coast of New Zealand's South Island, is a fjord. It is a finger-like inlet surrounded by sheer walls that rise 1,200 m (3,900 ft) above sea level and plunge to depths of 500 m (1,640 ft). Its entrance is only 55 m (180 ft) deep. As in other fjords, the shallow entrance restricts the exchange of water between the fjord and the open sea, resulting in stagnant, oxygen-depleted, deep water.

PHYSICAL CHARACTERISTICS OF ESTUARIES

Influenced by the tides and the mixing of fresh and salt water, estuaries have a unique combination of physical and chemical characteristics. These factors govern the lives of the organisms that live there.

Salinity

The salinity of estuaries fluctuates dramatically both from place to place and from time to time. When seawater, averaging about 35‰ salinity, mixes with fresh water (nearly 0‰) the mixture has a salinity somewhere in between. The more fresh water that is mixed in, the lower the salinity. Salinity therefore decreases as one moves upstream (Fig. 12.3).

Salinity also varies with depth in the estuary. The salty seawater is more dense and stays on the bottom (see "Salinity, Temperature, and Density," p. 45). It flows in along the bottom in what is frequently known as a **salt wedge.** Meanwhile, the fresher, less dense water from the river flows out on the surface.

The salt wedge moves back and forth with the daily rhythm of the tides (Fig. 12.4). It moves up the estuary on the rising tide, then recedes as the tide falls. This means that organisms that stay in one place are faced with dramatic fluctuations in salinity. They are submerged under the salt wedge at high tide and under low-salinity water at low tide. If the area has a **diurnal tide,** the organisms are subjected to two shifts in salinity every day: one as the tide moves upstream and a second as it retreats. In an estuary with **semidiurnal tides,** salinity changes four times a day.

> Estuaries are subject to wide fluctuations in salinity.

The behavior of water masses in estuaries is not always this simple. The shape of the estuary and its bottom, the wind, evaporation of water from the surface, and changes in the tide all influence the distribution of salinity. Also of importance are seasonal variations in freshwater runoff from rivers as a result of rainfall patterns or snowmelt. Currents are especially important. Because most estuaries are long and narrow, the tide doesn't just rise; it rushes in, often creating strong **tidal currents.** In a few places the tide actually comes in as a nearly vertical wall of water known as a **tidal bore.** Tidal bores in the Qiantang River, China, can generate waves as high as 6 m (20 ft)! Such strong water movements greatly affect the pattern of salinity in an estuary.

Another factor that affects circulation in estuaries is the **Coriolis effect.** North of the Equator, the fresh water that flows from rivers toward the sea is deflected toward the right. South of the Equator, the flow is to the left. This means that in estuaries located

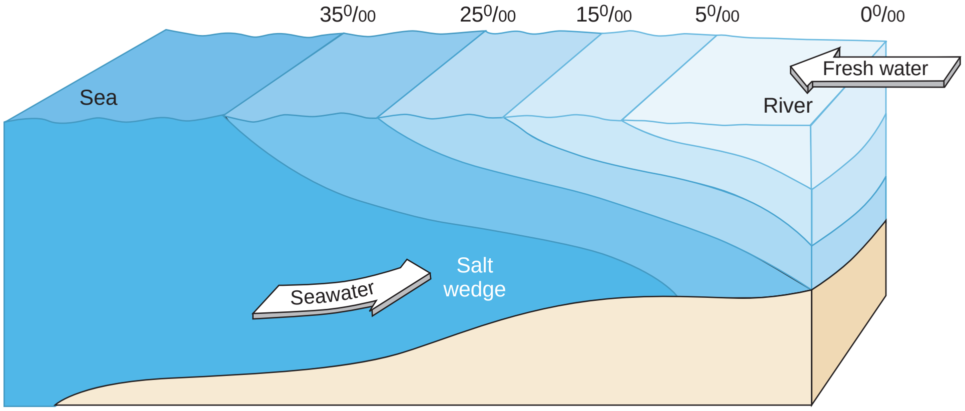


FIGURE 12.3 Profile of an idealized estuary. The lines across the estuary connect points of similar salinity and are known as *isohalines.*

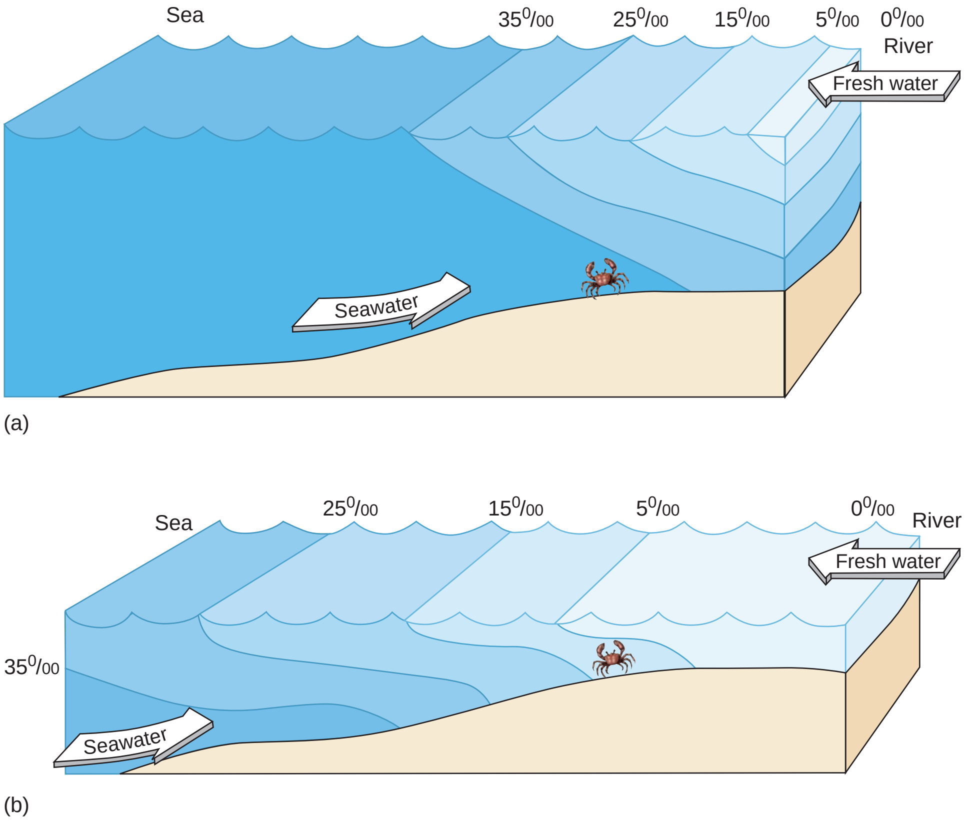


FIGURE 12.4 The salt wedge in a typical estuary moves in and out with the tide. (*a*) At high tide the crab is covered by water with a salinity of 35%. (*b*) At low tide it is covered by water with a low salinity, between 5‰ and 15‰.

Plate Tectonics The process in which large sections of the earth's crust move about.
- Chapter 2, p. 23

Passive Continental Margin One that is on the "trailing edge" of a continent and therefore has little geological activity.
- Chapter 2, p. 35; Figure 2.22

Active Continental Margin One that is colliding with another plate and therefore has a lot of geological activity.
- Chapter 2, p. 34; Figure 2.22

Semidiurnal Tide A tidal pattern with two high and two low tides each day.
Diurnal Tide A tidal pattern with one high and one low tide each day.
Mixed Semidiurnal Tide A tidal pattern in which two successive high tides are of different heights.
- Chapter 3, p. 61; Figure 3.34

Coriolis Effect As a result of the earth's rotation, anything that moves large distances on the earth's surface tends to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.
- Chapter 3, p. 49

in the Northern Hemisphere marine organisms can penetrate farther upstream on the left side when one faces seaward. In the Southern Hemisphere they extend up the right side.

In regions of little freshwater runoff and high evaporation, the salinity of the water increases. An example is Laguna Madre, a shallow bar-built estuary with limited access to the open ocean that parallels the Texas coast for 185 km (115 mi). The average salinity is over 50‰ in some areas, and it may reach 100‰ or more during dry spells. These high-salinity estuaries are called **negative estuaries**.

Substrate

Rivers carry large amounts of sediment and other materials, including pollutants, into most estuaries. Sand and other coarse material settle out in the upper reaches of the estuary when the river current slows. The fine, muddy particles, however, are carried further down the estuary. There, many of them settle out when the current slows even more, though the finest particles may be carried far out to sea. The **substrate,** or type of bottom, of most estuaries is therefore sand or soft mud.

Mud, which is actually a combination of silt and clay (see Fig. 11.27), is rich in organic material. As in other organic-rich sediments, respiration by decay bacteria uses up oxygen in the **interstitial water,** the water between sediment particles. Water cannot easily flow through the fine sediments to replenish the oxygen supply. As a result, the sediments in estuaries are often devoid of oxygen, or are **anoxic,** below the first few centimeters (see Fig. 11.29). They have the black color and rotten-egg smell typical of anoxic sediments, in which **hydrogen sulfide (H_2S),** which is toxic to most organisms, accumulates. Anoxic sediments are not completely devoid of life. **Anaerobic bacteria,** which do not need oxygen to carry out respiration, thrive under these conditions.

Fine, muddy sediments brought into estuaries by rivers settle out in the relatively quiet waters. Bacterial respiration in these organic-rich sediments depletes the oxygen in them.

In estuaries that have unimpeded tidal flow, which includes most shallow ones, there is plenty of oxygen dissolved in the water. Some deep-water estuaries such as fjords (see Fig. 12.2), however, have a shallow "sill" at the entrance that restricts water circulation. Low-salinity water flows out unimpeded on the surface. The sill, however, prevents seawater from flowing in along the bottom. The stagnant deep water may become depleted in oxygen because of bacterial respiration associated with the decomposition of organic matter that sinks and accumulates on the bottom.

Other Physical Factors

Water temperature in estuaries, except fjords, varies markedly because of their shallow depths and large surface area. Organisms that are exposed at low tide may have to face even more drastic daily and seasonal temperature fluctuations.

Large amounts of suspended sediments are typical of estuaries, greatly reducing the water clarity. Very little light thus penetrates through the water column. The particulate material in the water can also clog the feeding surfaces of some filter feeders and even kill organisms, such as some sponges, that are sensitive to sediment.

ESTUARIES AS ECOSYSTEMS

To the uninitiated, an estuary may at first look like a wasteland. This impression is far from the truth. Estuaries are tremendously productive and are home to large numbers of organisms, many of which are of commercial importance. Estuaries also provide vital breeding and feeding grounds for many birds, fishes, shrimps, and other animals. Estuarine ecosystems consist of several distinct communities, each with its own characteristic assemblage of organisms.

Living in an Estuary

Life in an estuary revolves largely around the need to adapt to extremes in salinity, temperature, and other physical factors. Though other marine environments may be more extreme—they may be colder or more saline, for instance—none changes so rapidly or in so many ways as an estuary. Living in an estuary is not easy, so relatively few species have successfully adapted to estuarine conditions.

Coping with Salinity Fluctuations Maintaining the proper salt and water balance of cells and body fluids is one of the greatest challenges facing estuarine organisms. Most estuarine organisms are marine species that have developed the ability to tolerate low salinities (Fig. 12.5). How far they can move up the estuary depends on just how tolerant they are. Most estuarine

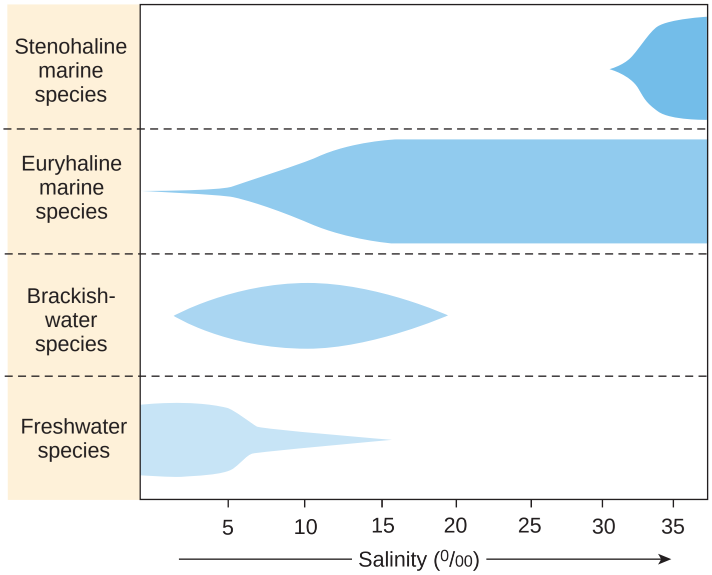


FIGURE 12.5 Types of species living in an idealized estuary in relation to salinity. The width of the bars represents the relative number of species.

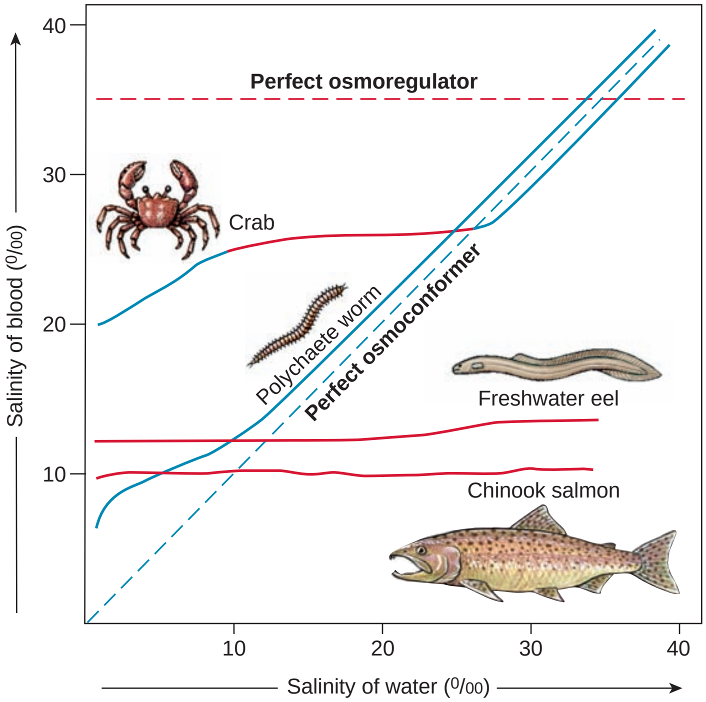


FIGURE 12.6 The salinity of the body fluids of estuarine animals responds in various ways to the salinity of the surrounding water. In a perfect osmoconformer, the salinity of the blood exactly matches that of the water. In a perfect osmoregulator, blood salinity stays the same no matter what the water salinity is. We have drawn the line for an imaginary perfect osmoregulator at 35‰. The salmon and freshwater eel are nearly perfect osmoregulators even though their bloods are more dilute. The important point is not the actual salinity of the blood but the fact that it remains relatively constant. Notice that some organisms, like the crab in the diagram, can only osmoregulate within a certain range of salinity; they are osmoconformers outside this range.

organisms are **euryhaline** species, that is, they tolerate a wide range of salinities. The relatively few **stenohaline** species, those that tolerate only a narrow range of salinities, are limited to the upper or lower ends of the estuary and rarely penetrate into the estuary proper. Stenohaline species can be either marine or freshwater in origin. Some species are adapted to live in **brackish water,** or water of intermediate salinity. Some of these species are stenohaline; others are euryhaline.

Because of their marine background, most estuarine organisms face the problem of the water in estuaries being diluted with fresh water. Those having an internal salt concentration higher than that of the surrounding water tend to take on water through **osmosis** (see Fig. 4.13*a*). Some animals adapt by simple changes in behavior. They may hide in their mud burrows, close their shells, or swim away if the salinity drops. These strategies are not widespread in estuaries, however, and most organisms rely on other mechanisms.

FIGURE 12.7 Cordgrass (*Spartina*) is an important component of salt marshes on both the Atlantic and Pacific coasts of North America and other temperate shores worldwide.

Soft-bodied estuarine animals, such as many molluscs and polychaete worms, often maintain osmotic balance simply by allowing their body fluids to change with the salinity of the water. They are called **osmoconformers** (Fig. 12.6). Many fishes, crabs, molluscs, and polychaetes are instead **osmoregulators.** They keep the salt concentration of their body fluids more or less constant regardless of the water salinity. When the salinity of the water is lower than that of the blood, they get rid of excess water and, via **active transport,** absorb some solutes from the surrounding water to compensate for those lost in the elimination of water. The gills, kidneys, and other structures accomplish this.

Bony fishes that inhabit estuaries also need to osmoregulate, since their blood is less salty than seawater (see Fig. 4.14 and "Regulation of the Internal Environment," p. 164). Salmon and freshwater eels migrate back and forth between rivers and the sea and still maintain a stable internal environment, thanks to the active transport of solutes by their kidneys and gills.

Organisms in estuaries have adapted to salinity fluctuations in various ways. Osmoconformers let the salinity of their body fluids vary with that of the water. Osmoregulators keep the salt concentration of their body fluids constant.

Few animals can be neatly classified as perfect osmoconformers or perfect osmoregulators. Many invertebrates, for instance, osmoregulate at low salinities and osmoconform at higher salinities. Even efficient osmoregulators such as salmon and freshwater eels do not keep *exactly* the same concentration of salts and other solutes in their blood as salinity changes.

Estuarine plants must also handle salinity variations. Grasses and other salt-marsh plants are land plants that have developed high salt tolerance. Some of these plants actively absorb salts and concentrate harmless solutes like sugars to match the outside concentrations and prevent water from leaving their tissues. Notice that this is opposite to the situation in marine organisms that live in estuaries, which have to adapt to reduced, not increased, salinities.

Different adaptations have evolved in some estuarine plants. Cordgrasses (*Spartina;* Fig. 12.7), other salt-marsh plants, and some mangroves actually excrete excess salts by way of salt glands in their leaves. Some estuarine plants, such as pickleweed

Osmosis The movement of water from high to low concentrations across a membrane.
Active Transport The transfer of substances across membranes by a cell against a *concentration gradient.*
- Chapter 4, p. 72

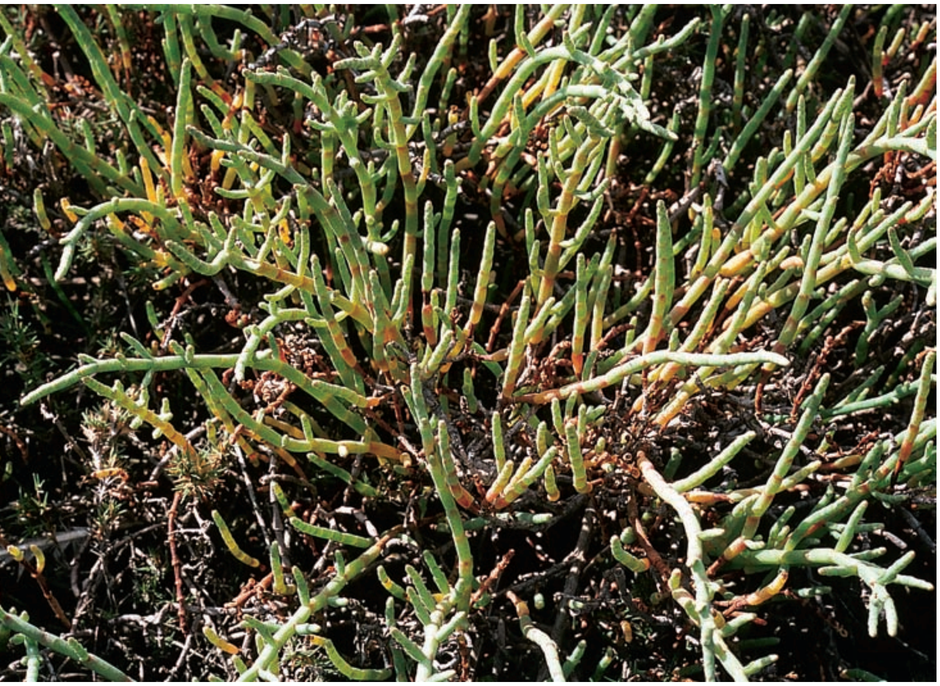


FIGURE 12.8 Pickleweed (*Salicornia* is) a common succulent plant in salt marshes around the world.

(*Salicornia*), accumulate large amounts of water to dilute the salts they take up (Fig. 12.8). Fleshy plants such as these are known as **succulents.**

Adapting to the Mud As discussed in Chapter 11 (see "Living in the Sediment," p. 260), living in mud has its problems. There is nothing to hold on to, so most animals either burrow or live in permanent tubes beneath the sediment surface. Clams do well because they can extend their siphons through the mud to get water for food and oxygen. Because it is difficult to move through mud, the inhabitants tend to be stationary or slow-moving. Living in mud, however, has a benefit: Salinity fluctuations are less drastic than in the water column.

The depletion of oxygen caused by the decay of organic matter in the mud presents another challenge. This is no problem to burrowers that pump oxygen-rich water into their burrows. Burrowers without this luxury have special adaptations to low-oxygen environments. Some have blood that contains **hemoglobin,** which has a particularly high affinity for oxygen. It can hold and carry oxygen even when only minute quantities are available. Some clams and a few other mud-dwellers can even survive for days without oxygen.

Types of Estuarine Communities

Several distinct communities are associated with estuaries. One consists of the **plankton,** fishes, and other open-water organisms that come in and leave with the tide. Several other communities are permanent parts of the ecosystem.

Estuarine communities consist of relatively few species. These species, however, are typically represented by many individuals. A surprising number of estuarine species, particularly those inhabiting temperate estuaries, are widely distributed around the world. Many have been distributed by humans, often with undesirable consequences.

Open Water The type and abundance of plankton inhabiting estuaries vary tremendously with the currents, salinity, and temperature. The murky water restricts the penetration of light and may limit **primary production** by phytoplankton. Most of the phytoplankton and zooplankton in small estuaries are marine species flushed in and out by the tides. Larger estuaries may also have their own, strictly estuarine, species.

One reason many of the world's great cities developed around estuaries is the rich supply of fish and shellfish in or near estuaries. Many species of commercially important fishes and shrimps use estuaries as nurseries for their young, taking advantage of the abundant food and relative safety from predators. About 90% of the marine commercial catch in the northern Gulf of Mexico, for example, is of species that depend on estuaries at some point in their lives.

A relatively rich variety of fishes live in most estuaries. Many are the juveniles of marine species that breed at sea but use estuaries as nurseries. Examples are the menhaden (Fig. 12.9), anchovies, mullets, croakers, and many species of flatfishes. Some fishes move through estuaries during their migrations. Such fishes are either **anadromous**—like salmon, smelts, and shad—or **catadromous**—like freshwater eels. Relatively few fishes spend their entire lives in estuaries. Killifishes (*Fundulus*) are one example.

Shrimps and crabs are often common in estuaries, and many commercially valuable species use estuaries as nurseries.

Mudflats The bottoms of estuaries that become exposed at low tide often form **mudflats** (see Fig. 12.14 and photo on p. 265). Mudflats are especially extensive in estuaries where there is a large **tidal range** and a gently sloping bottom. It all looks pretty much the same, but the mudflat can vary widely in particle size. Sand may accumulate to create sand flats near river mouths and in the tidal creeks that form as the tide changes. In the calmer central part the mudflat contains more fine, silty material.

Mudflat communities in estuaries are similar to those on muddy shores (see "Soft-Bottom Intertidal Communities," p. 259). Low tides expose organisms to desiccation, wide variations in temperature, and predation, just as in any other intertidal community. In estuaries, however, mudflat organisms must also withstand regular variations in salinity.

Primary producers are not usually evident on mudflats. A few hardy seaweeds—such as the green algae *Enteromorpha* (Fig. 12.10) and *Ulva,* the sea lettuce, and the red alga *Gracilaria*—manage to grow on bits of shell. These and other primary producers may be particularly common during the warmer months. Large numbers of benthic diatoms grow on the mud and

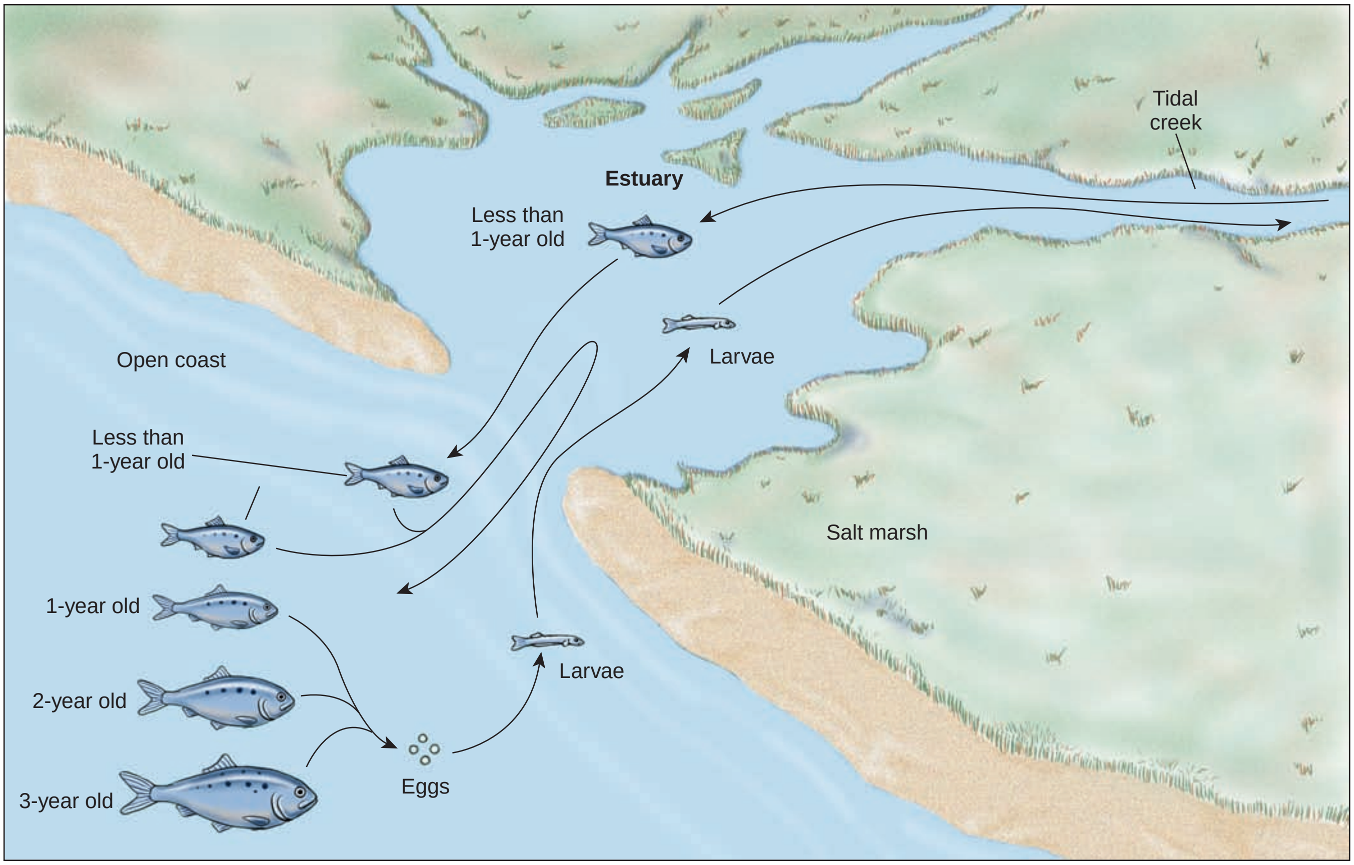


FIGURE 12.9 The Atlantic menhaden (*Brevoortia tyrannus*) is one of the most important commercial fishes in the United States. Adult fish (one to three years old) spawn offshore and the larvae drift with the tides and currents into estuaries, moving into shallow areas in the salt marshes to grow.

often undergo extensive blooms, forming golden-brown patches. In tide pools left by the receding tides these patches become coated with oxygen bubbles as intense photosynthesis takes place in the sunlight.

FIGURE 12.10 The California horn snail (*Cerithidea californica*), a deposit feeder, is abundant on mudflats. The green alga is *Enteromorpha,* which tolerates wide fluctuations in salinity and temperature as well as pollution. It can be found on rocky shores as well as along the shores of estuaries. It thrives during the long, sunny days of summer, when it can turn mudflats into bright-green "meadows."

Bacteria are extremely abundant on mudflats. They decompose the huge amounts of organic matter brought in by rivers and tides. When the oxygen is used up by decay, some bacteria produce hydrogen sulfide. This in turn is used by

Hemoglobin A blood protein that transports oxygen in many animals; in vertebrates it is contained in *erythrocytes,* or red blood cells.
- Chapter 8, p. 164

Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Primary Production The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs—that is, the production of food.
- Chapter 4, p. 68

Anadromous Fishes Those that migrate from the sea to spawn in fresh water.
- Chapter 8, p. 168

Catadromous Fishes Those that migrate from fresh water to spawn at sea.
- Chapter 8, p. 169

Tidal Range Difference in water level between successive high and low tides.
- Chapter 3, p. 60

sulfur bacteria, chemosynthetic bacteria that derive energy by breaking down sulfur compounds such as hydrogen sulfide (see Table 5.1, p. 88). Diatoms and bacteria, including photosynthetic bacteria, actually account for most of the primary production on mudflats.

The dominant animals on mudflats burrow in the sediment and are known as **infauna** (Fig. 12.11). Though there are not many species of these burrowing animals, they often occur in immense numbers. At low tide their presence may be revealed only by small sediment mounds topped by a hole or piles of feces and other refuse. They feed on the abundant **detritus** in the sediment and water. Most of the food for these animals is brought in by the rivers and tides and is not actually produced on the mudflat. Very few mudflat animals can be classified as **epifauna,** those that either live *on* the sediment surface or are attached to a surface as **sessile** forms.

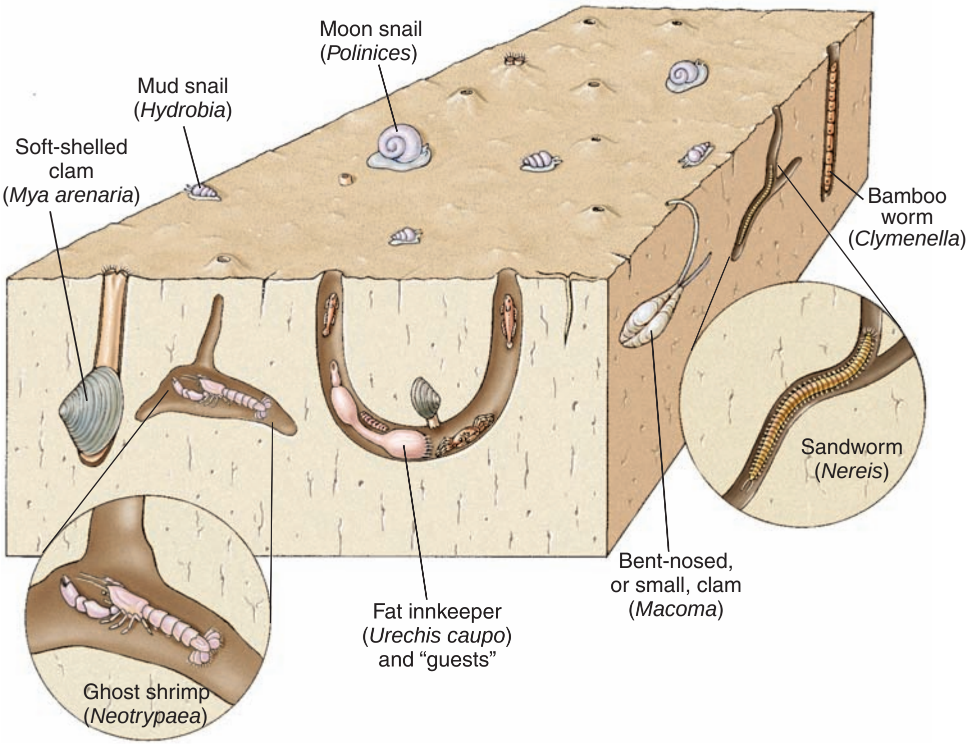


FIGURE 12.11 Some representative inhabitants of mudflats in temperate estuaries. Many mudflat organisms also can be found on muddy bottoms outside estuaries (also see Fig. 13.6).

Mudflat inhabitants that feed on detritus are **deposit** and **suspension feeders,** including **filter feeders.** Deposit feeders are more common than suspension feeders on mudflats and other muddy bottoms (see Fig. 13.12). Suspension feeders are at a disadvantage because their filtering mechanisms tend to get clogged by the high amounts of sediment that rains on soft bottoms. Furthermore, deposit feeders actually exclude many suspension feeders by disturbing the sediments, which clogs the suspension feeders' feeding structures and buries their newly settled larvae.

Suspension feeders, on the other hand, dominate where the sediment is more sandy. The wider interstitial spaces between the larger sand particles hold less detritus for deposit feeders to eat, and the abrasive sand is hard on their digestive systems.

The dominant primary producers on mudflats are diatoms and bacteria. Most of the animals are burrowing deposit and suspension feeders that feed on detritus.

Protozoans, nematodes, and many other minute animals that compose the **meiofauna** (see "Life in Mud and Sand," p. 291) also thrive on detritus. The meiofauna are also known as **interstitial** animals. The larger burrowing animals, or infauna, include many polychaetes (see Figs. 11.31 and 12.11). Most are deposit feeders. Other polychaetes are suspension feeders that filter water or extrude tentacles to collect the detritus that falls from the water column. Yet another detritus-feeding strategy among some polychaetes is to switch back and forth between suspension and deposit feeding, depending on the amount of suspended material in the water.

Bivalves often abound on mudflats. Many are filter feeders that are also found on muddy and sandy shores outside estuaries (see Fig. 11.30). Examples from temperate waters are the quahog, or hard clam (*Mercenaria mercenaria*), the soft-shelled clam (*Mya arenaria;* Fig. 12.11), and razor clams (*Ensis*). Some of these are of considerable commercial importance. Bent-nosed, or small, clams (*Macoma;* Fig. 12.11) are deposit feeders that use their long incurrent siphons to vacuum the surface.

The ghost (*Neotrypaea,* Fig. 12.11) and mud (*Upogebia*) shrimps make elaborate burrows that, as a side effect, help oxygenate the sediment. These shrimps feed on detritus that they filter from the water and sift from the mud. Fiddler crabs (*Uca*) also live in burrows but are active on the mudflats at low tide (see "Fiddler on the Mud," p. 273). They process the mud and extract the detritus, which they eat.

On the Pacific coast of North America the fat innkeeper (*Urechis caupo;* Fig. 12.11), an echiuran worm, secretes a funnel-shaped net of mucus. It pumps water through this net to filter out food. It gets its common name because it shares its U-shaped burrow with a polychaete (*Hesperonoe adventor*), a crab (*Scleroplax granulata*), one or more fish (*Clevelandia ios*), and other guests.

Some animals live on the surface of the mud or move in and out with the tide. These include deposit feeders such as mud snails (*Cerithidea, Hydrobia;* Figs. 12.10 and 12.11), amphipods, and shrimps. Carnivores include polychaete worms (*Nereis;* Fig. 12.11), moon snails (*Polinices;* Fig. 12.11) and other predatory snails (*Busycon*), and swimming crabs (*Callinectes*).

By far the most important predators in the mudflat community are fishes and birds. Fishes invade mudflats at high tide, whereas birds congregate at low tide to feed. Estuaries are important stopover

Fiddler on the Mud

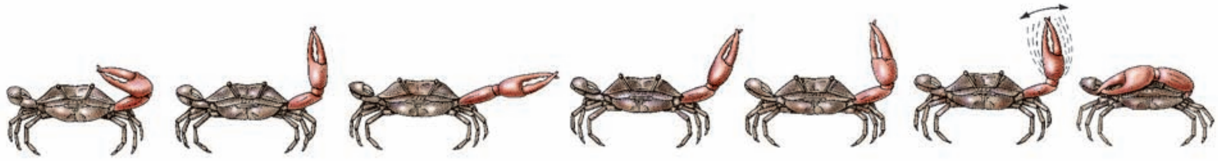
What lives in mud, literally feeds on mud, and finds mates by calling and waving across the mud? But, of course—fiddler crabs, creatures remarkable in many ways but best known as the ultimate experts in mud.

The many species of fiddler crabs (*Uca*) are inhabitants of mud and sand flats in estuaries and other sheltered coasts. They are found mostly in the tropics and subtropics, but some species are found as far as Southern California and Boston Harbor. Fiddlers are deposit feeders. They feed at low tide, using their pincers to scoop mud up into feeding appendages close to the mouth. The detritus in the mud is extracted with the help of brush-like mouthparts. Water is pumped from the gill chambers into the mouth to make the lighter detritus float and thus help separate it from the mud. The detritus is swallowed, and the clean mud is spat out on the substrate in neat little balls.

Fiddlers are active at low tide and retreat into their burrows at high tide. Each burrow has an entrance (revealed by the neat little balls of mud around it) that the occupant can plug when the tide comes in. At the next low tide, crabs emerge from home to feed and do whatever healthy, active fiddlers like to do. The tidal cycle means everything to them. Tides are so crucial that if crabs are taken away and isolated in an environment of constant light and temperature, they will continue to be active at the times that correspond to low tide and sit quietly when they were expected to be at home! Not only activity patterns but color changes that normally take place in their natural environment (darker color during the day, lighter at night) continue to be observed in isolation. These patterns are examples of **biological clocks,** repeated rhythms that are synchronized with time. In the case of fiddlers, activity patterns and color changes are synchronized with tides, which depend on lunar cycles, and with day-night changes, which depend on the sun.

Fiddlers also have an interesting sex life. Males feature one tremendously enlarged claw, either right or left. It is brightly colored or highlighted with markings in many species. Females have a much smaller pair of claws that are used in feeding, as is the males' small pincer. Males use their big claw to advertise their sex—to tell females they mean business and to threaten any other males that may be in their way. They wave the claw at low tide on territories established around their burrows. In one species, males build a mud shelter around the burrow to heighten the effect. Claw-waving gets so heated sometimes that a whole mudflat seems to move up and down with hundreds of displaying males. Males entice any interested females into their burrows, and a female may visit a few pads before deciding on a particular one. Males often fight for prospective mates but are also known to establish partnerships with neighbor males to defend their territories against intruders. Fighting with a stronger neighbor may cause a fiddler to end up with a lost claw, a more costly alternative than peaceful cooperation. A lost claw means disaster. It takes many molts to regenerate one that is big enough to get the crab back in action, and crabs whose claws are too small or that don't have the right moves can get pretty lonely!

In those areas coinhabited by several species of fiddlers, waving is used to prevent a male from attracting females of the wrong species. Some species wave up and down, others sideways. The angle and frequency of waving also vary, and bowing, fancy steps, and other body movements may form part of the ritual. Some beat the claw on the ground, and males of many species even produce sound by vibrating a joint of the large claw. It pays to advertise!



Signaling in a male fiddler crab (*Uca*).

and wintering areas for many species of migratory birds. The open spaces offer them safety from natural enemies, and food is plentiful. The most significant predators on mudflats are wading shorebirds (Figs. 12.12 and 12.13). These include the willet, godwits, dowitchers, and many species of plovers and sandpipers. They feed on polychaetes, ghost shrimps and other small crustaceans, clams, and mud snails. Oystercatchers specialize on clams and other bivalves.

These birds do not all exploit the same type of prey. The varying lengths of their bills represent a specialization in prey because different types of prey live at different depths in the mud (Fig. 12.12). In addition, shorebirds use different strategies to locate their food. Birds such as sandpipers rely mostly on their bills, probing in the mud as they walk around (Fig. 12.13*a*). Others, like plovers, use their eyesight to detect slight movements on the surface of the mud (Fig. 12.13*b*). Some biologists think that these differences in feeding habits are an example of **resource partitioning.**

Herons and egrets compose yet another group of wading birds. They specialize in catching fishes, shrimps, and other small

Chemosynthetic Bacteria *Autotrophic bacteria* that use energy contained in inorganic compounds rather than sunlight to make organic matter.
- Chapter 5, p. 92; Table 5.1

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

Deposit Feeders Animals that feed on organic matter that settles in the sediment.
Suspension Feeders Animals, including *filter feeders,* that feed on particles suspended in the water column.
- Chapter 7, p. 116; Figure 7.3

Resource Partitioning The sharing of a resource by two or more species to avoid competition.
- Chapter 10, p. 214

swimming prey. Birds that feed by swimming or diving in the estuary, such as ducks, terns, and gulls, are often seen resting on mudflats.

Salt Marshes Estuaries in temperate and subarctic regions are usually bordered by extensive grassy areas that extend inland from the mudflats. These areas are partially flooded at high tide and are known as **salt,** or **tidal, marshes** (Fig. 12.14). Sometimes they are grouped with coastal environments flooded at high tide and with freshwater marshes and collectively called **wetlands.** Though mostly associated with estuaries, salt marshes can also develop along sheltered open coasts. They develop as long as disturbance from wave action is minimal to allow the accumulation of muddy sediments. Tidal creeks, freshwater streams, and shallow pools frequently cut through the marsh.

In North America, salt marshes are particularly extensive along the Atlantic and Gulf coasts (see Fig. 2.22). The broad estuaries and shallow bays of these gently sloping coastlines provide optimal conditions for the development of salt marshes. The Pacific coast of North America, on the other hand, is generally steeper, and most of the estuaries have formed along narrow river valleys. This has resulted in less extensive development of salt marshes. In the Northern Hemisphere salt marshes tend to be more extensive on the left side than on the right side of estuaries, since the turbulence caused by the flow of freshwater from rivers is stronger on the right side as a result of the Coriolis effect.

Salt marshes are subject to the same extremes in salinity, temperature, and tides that affect mudflats. They also have a muddy bottom, but it is held together by the roots of marsh plants and thus is more stable.

Salt-marsh communities are dominated by a few hardy grasses and other salt-tolerant land plants. These plants thrive in the marsh, though the environment is too harsh for most other land plants. There is a pronounced zonation of plants in salt marshes (Fig. 12.15). The location of a given zone is related to the height relative to the tide, but it varies according to geographical location, type of substrate, and other factors. For instance, soil salinity may become particularly high

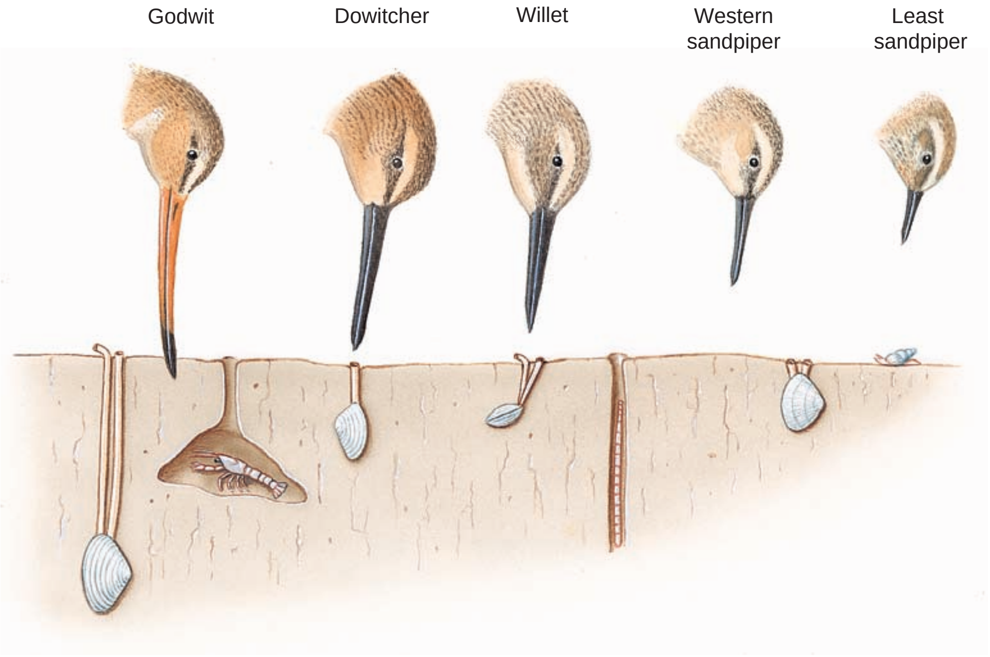


FIGURE 12.12 Differences in the bill length of wading shorebirds from the west coast of North America allow them to feed on particular mudflat animals.

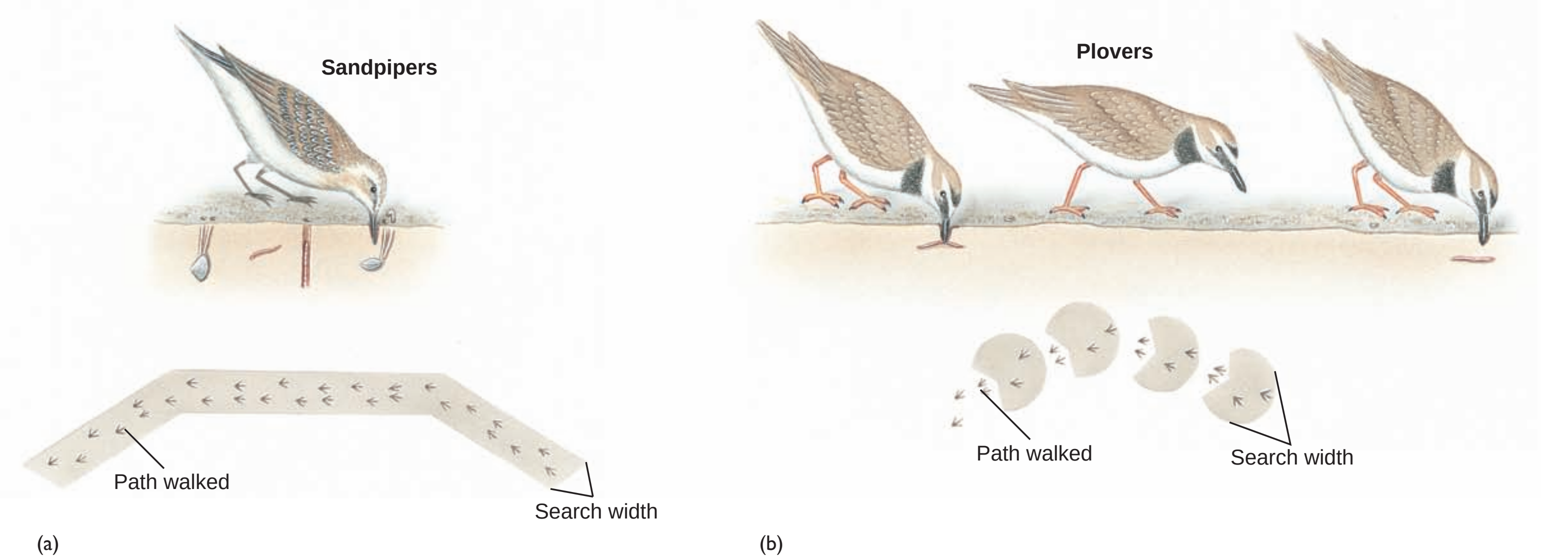


FIGURE 12.13 Feeding behavior also varies among shorebirds. (*a*) Sandpipers use their bills to search for food and follow a roughly straight path. (*b*) Plovers rely mostly on their vision, turning their heads sideways as they move.

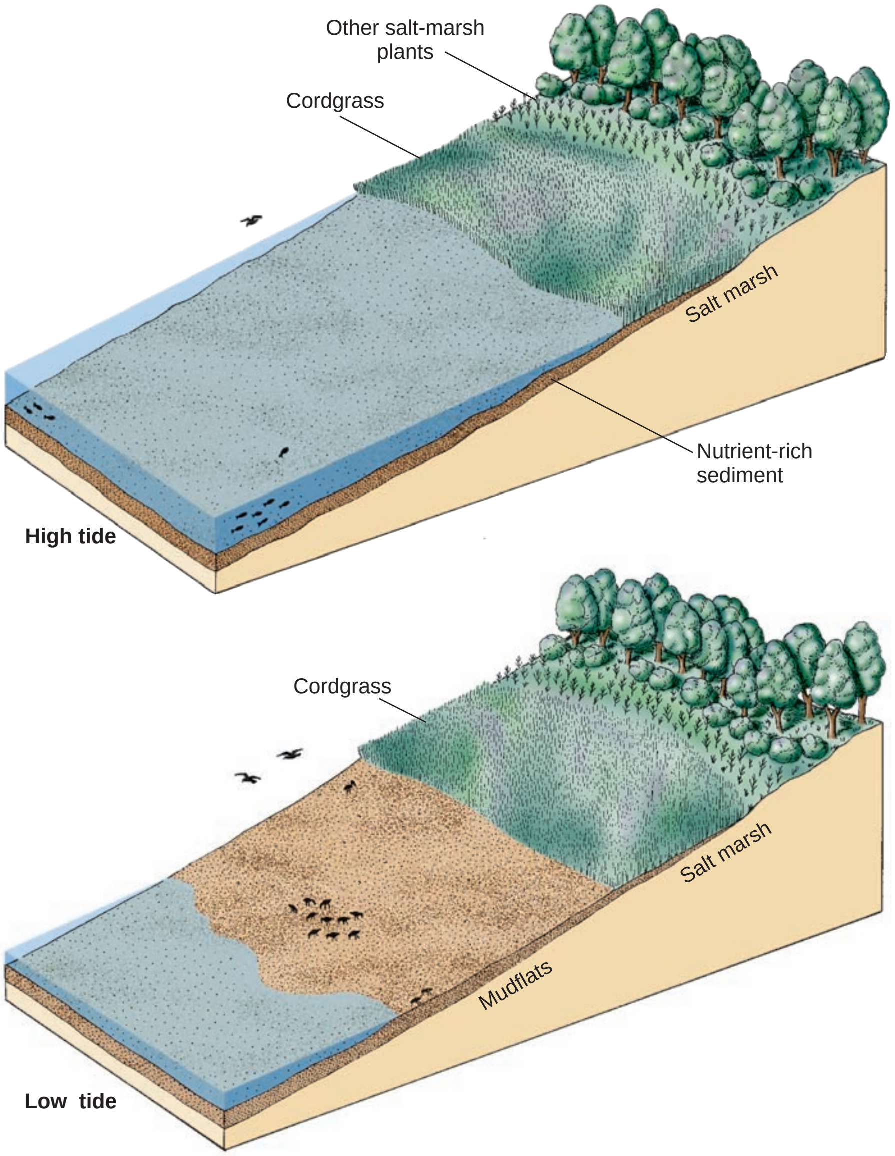


FIGURE 12.14 The daily tides play a crucial role in salt marshes. They help circulate detritus and nutrients and expose mudflat organisms to predation by shorebirds and other animals.

at intermediate heights as a result of higher evaporation in marshes closer to hot, dry regions. This may result in areas bare of vegetation.

Cordgrasses (the smooth cordgrass, *Spartina alterniflora*, on the Atlantic coast; the California cordgrass, *S. foliosa,* on the Pacific coast; see Fig. 12.7) are typically the most common plants along the seaward limit of the salt marsh, where it meets the mudflats (Figs. 12.14 and 12.15). These grasses invariably occupy the fringe above the mean low tide level. Plants do better here because the soil is well drained and therefore richer in oxygen and less salty. The tops of their tall leaves remain exposed to the air even when the bottom is covered at high tide. The plants have extensive horizontal stems that stretch out underground. The leaves and roots develop from the stems. Roots just below the soil may take in oxygen from the air.

Cordgrass may gradually invade mudflats because the plants slow down the tidal flow and thus increase the amount of sediment trapped among the roots. The landward extension of the salt marsh is eventually limited by the height of the highest tide. In addition to providing a significant portion of the high primary production of estuarine communities (see "Feeding Interactions among Estuarine Organisms," p. 279), salt-marsh plants like cordgrass help stabilize soils by decreasing the effects of wave action. Smooth cordgrass from the Atlantic has been introduced in other parts of the world for the protection of shorelines, sometimes with negative effects (see "Biological Control of Invasive Cordgrass," p. 276).

Cordgrass gives way to other plants in the higher parts of the marsh. On the Atlantic coast, a second species of cordgrass (the saltmeadow, or salt-marsh hay, *Spartina patens*) dominates (Fig. 12.15), but rushes (*Juncus*), pickleweed, and several other plants often form distinct zones. The higher levels of salt marshes on the Pacific coast are usually dominated by pickleweed (see Fig. 12.8). The landward limit of salt marshes is a transition zone with adjacent terrestrial, or land, communities. It is characterized by a large variety of plants resistant to salt spray, such as salt grasses (*Distichlis*) and several species of pickleweed. It appears that in most salt marshes zonation is determined not only by the effects of flooding by tides but also by the combined effect of other factors. They include competition for space among salt-marsh plants, increased soil salinity in warm areas due to evaporation, and even the effect of burrowing animals.

The muddy salt-marsh substrate is home to decay bacteria, diatoms, and thick mats of filamentous green algae and cyanobacteria. Bacteria play a crucial role by decomposing the large amounts of dead plant material produced in the salt marsh. These bacteria and the partially broken-down organic matter are a major source of the detritus that feeds many of the inhabitants of the estuary. Some bacteria are **nitrogen fixers** that enrich the sediment.

Salt marshes are dominated by grasses and other marsh plants. Bacteria in the mud decompose dead plant material and contribute a large portion of the detritus in the estuary.

Some burrowing animals of mudflats also inhabit salt marshes. In addition, nematodes, small crustaceans, larvae of land insects, and other small invertebrates live among the algal mats and decaying marsh plants. Crabs are conspicuous inhabitants of salt marshes. Fiddler crabs build burrows along the mudflat edges, where they increase the oxygenation of soils. Other marsh crabs (*Sesarma,*

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.
- Chapter 5, p. 93; Table 5.1

EYE ON SCIENCE

Biological Control of Invasive Cordgrass

The smooth cordgrass (*Spartina alterniflora*), a native to the Atlantic coast of North America, has become a pest on the Pacific coast after its introduction there. As in the case of many **invasive species,** there are harmful effects resulting from its introduction elsewhere (see "Biological Invasions: The Uninvited Guests," p. 414). Smooth cordgrass seeds were probably accidentally introduced when oysters were transplanted to the Pacific coast. The plant was also introduced, though intentionally, in some areas to protect the coast from erosion, not only in North America but in other parts of the world. It has spread over mudflats, tidal creeks, oyster grounds, and eelgrass beds. As the plant spreads, more sediment is accumulated by its roots, turning natural habitats into marshy land within a decade or so.

Research by a University of California, Davis team, has shown that on the Pacific coast smooth cordgrass actually hybridizes with the native Pacific cordgrass (*Spartina foliosa*). The hybrids, which can be identified because they contain DNA from both species, are taller, spread into deeper water, and reproduce more agressively, releasing more pollen and seeds, than the native cordgrass. Spreading is accelerated by the fact that, unlike the native species, the smooth cordgrass can self-pollinate. Hybrids have also crossed with other hybrids, evolving into at least nine different genetic strains. These hybrids are by now the dominant cordgrass in many Pacific salt marshes and the native Pacific cordgrass may soon be officially declared an endangered species.

Several efforts to control and hopefully eradicate the smooth cordgrass on the Pacific coast have so far proved ineffective. Hand pulling takes time and special effort, because the large scale of the infestation and the muddy environment. Chemical herbicides may harm other forms of life. An alternative is to use **biological control,** or **biocontrol,** the use of predators or of disease-causing microbes to exclusively eat or harm a pest.

There are at least 22 species of insects that feed on the smooth cordgrass in its native Atlantic habitat but apparently none in its new habitat on the Pacific coast. It has been suggested that adaptations that have evolved in the smooth cordgrass to defend it from insects in its native habitat are no longer needed and these resources are used instead for growth and reproduction.

Already introduced is a planthopper (*Prokelisia marginata*), an insect that feeds and lay its eggs on cordgrass. Plants weaken and die because the insects feed on the plant's sap. Biological control obviously involves several risks, and the introduction of non-native insects from the Atlantic and Gulf regions is seen as a very risky solution since the insects could also harm the native cordgrass.

After several years of thorough laboratory testing to make sure that the planthopper does not feed on native plants or that it transmits diseases, the use of biocontrol in Willapa Bay in the state of Washington was approved by a technical advisory panel and by state and federal agencies. There is no native cordgrass in Willapa Bay but the smooth cordgrass has spread in the area since it was accidentally introduced from the Atlantic more than 100 years ago. The planthopper has been introduced in the bay and its effect on the smooth cordgrass is being carefully followed by a team of scientists from the University of Washington.

What kind of experiments should be carried out before a biocontrol insect or microorganism is released into a salt marsh? Once an insect is released, what type of observations should be regularly collected in the field?

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

Hemigrapsus) are scavengers that eat dead organic matter. Some of these species live in burrows.

Marsh plants provide shelter and food to many marine and land animals. Coffee bean snails (*Melampus*) and marsh periwinkles (*Littorina, Littoraria*) are air-breathing snails that feed on detritus, minute algae, and fungi that grow on marsh plants. They move up the plants as the high tide moves in. Though they are air-breathers, they lay their eggs in the water and the larvae that hatch develop in the plankton. The ribbed, or horse, mussel (*Geukensia demissa*) is a suspension feeder that lives half buried in the mud among the cordgrass (Fig. 12.16). Killifishes and juvenile silversides (*Menidia*) are examples of fishes that inhabit tidal creeks and pools in the marsh at low tide. They move into the salt-marsh grass at high tide to escape predators such as crabs and larger fishes, which enter the creeks with the rising tide. Crustaceans and small fishes retreat to pools or tidal creeks at low tide. Rails and American coots are among the birds that feed and nest here. Many other land birds and mammals, from ospreys to raccoons, are common visitors.

Mangrove Forests Mangrove forests are not limited to estuaries, but in some ways they are the tropical equivalents of salt marshes, though the two coexist in many places. **Mangroves** are flowering land plants adapted to live in the intertidal (see "Flowering Plants," p. 110). These trees and shrubs often form dense forests called **mangals** to distinguish them from mangroves, the actual plants themselves (see Figs. 6.14 and 6.15). Mangroves are typical of tropical and subtropical regions, where they replace the temperate salt marshes (Fig. 12.17 and foldout map). It has been estimated that around 75% of all sheltered tropical shores were at one time fringed with mangroves, a figure that suggests their tremendous importance. Mangrove forests, however, are being rapidly destroyed by humans (see "Human Impact on Estuarine Communities," p. 281).

Mangrove forests, or mangals, are formed by mangroves, tropical and subtropical trees and shrubs adapted to the intertidal environment.

Mangroves grow on protected coasts where muddy sediments accumulate. Though mangroves grow in estuaries, they are not restricted to them. As in salt-marsh plants, the various species of mangroves have different tolerances to immersion by high tide. Partly as a result of these differences in tolerance, they show a distinctive zonation in the intertidal, from a marine to a progressively terrestrial environment.

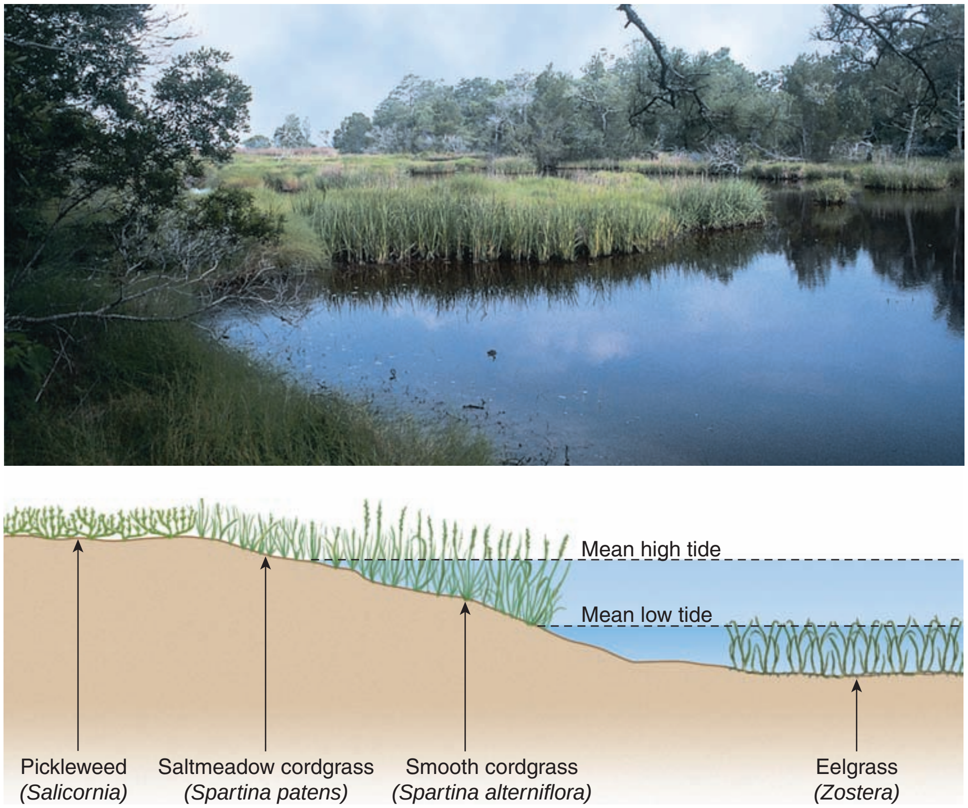

Mean high tide
Mean low tide
Pickleweed
(Salicornia)
Saltmeadow cordgrass
(Spartina patens)
Smooth cordgrass
(Spartina alterniflora)
Eelgrass
(Zostera)

FIGURE 12.15 A salt marsh near Atlantic Beach, North Carolina. As in other Atlantic marshes, the smooth cordgrass (*Spartina alterniflora*) occupies the edge of the marsh that is flooded the most by seawater. It is replaced higher up in the marsh by saltmeadow grass, or salt-marsh hay (*Spartina patens*), a shorter and finer grass that is less salt tolerant and may form extensive meadows. It grows where the marsh is flooded only at high tide. Many of these marshes have been filled in and destroyed.

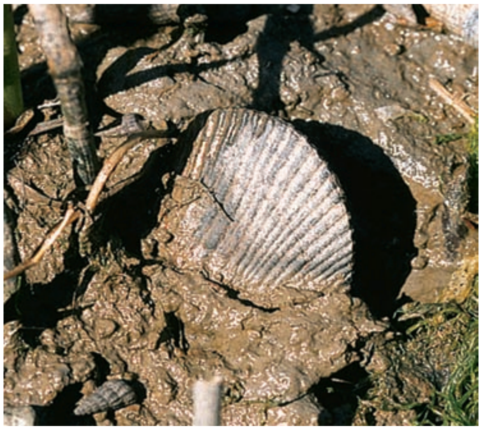


FIGURE 12.16 The Atlantic ribbed, or horse, mussel (*Geukensia demissa*) lives half buried in the mud. It has the unusual ability to slightly open its valves, or gape, at low tide and take in oxygen from the air.

Some mangroves need fresh water for growth. Since they live at the sea edge, mangroves must get rid of salts from the water that is taken in by the roots. Most salts are actually not taken in by the roots, and salt glands on the leaves of some species excrete salts.

The **Indo-West Pacific region** has the world's most extensive mangrove forests

Indo-West Pacific Region The tropical Indian and western and central Pacific oceans.
- Chapter 14, p. 315

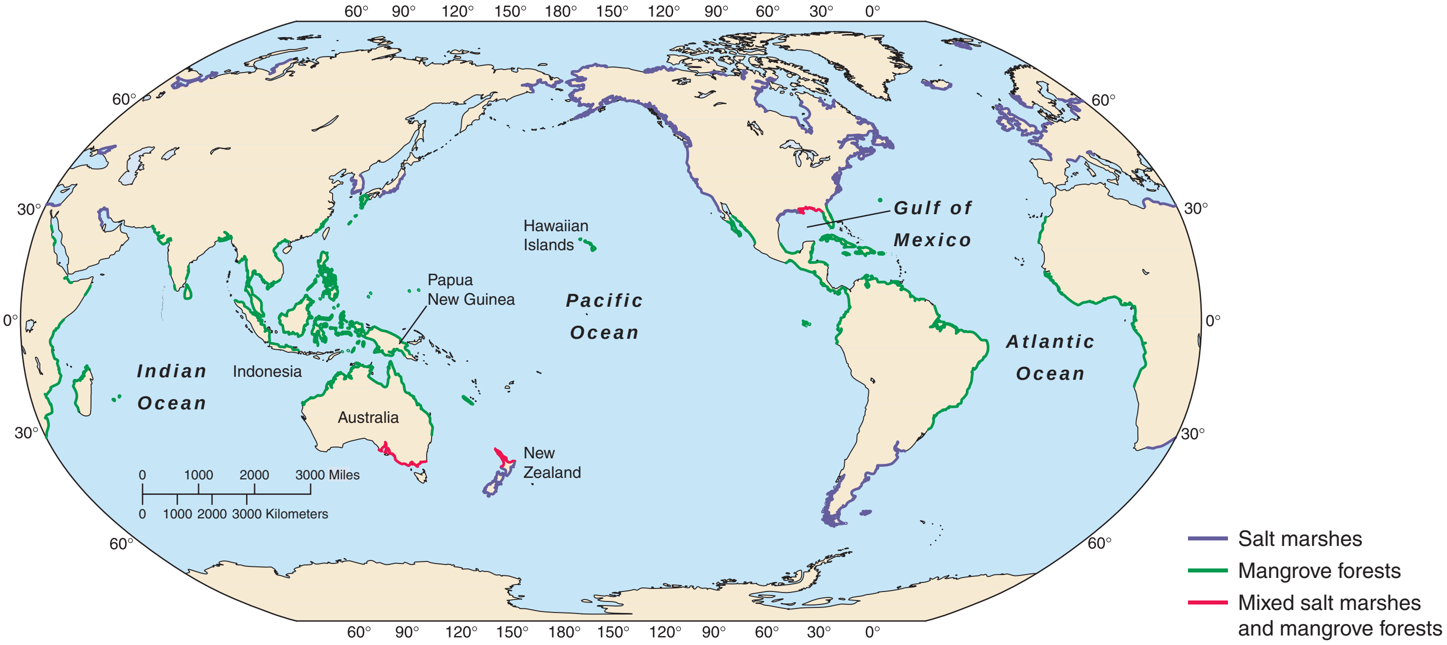

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60°
30°
0°
30°
60°
Hawaiian Islands
Papua New Guinea
Pacific Ocean
Gulf of Mexico
Atlantic Ocean
Indian Ocean
Indonesia
Australia
New Zealand
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
Salt marshes
Mangrove forests
Mixed salt marshes and mangrove forests

FIGURE 12.17 The world distribution of salt marshes and mangrove forests. Mangroves tend to replace salt marshes in tropical regions. The two overlap in such areas as the Gulf of Mexico, southern Australia, and New Zealand. Mangroves were introduced by humans to the Hawaiian Islands.

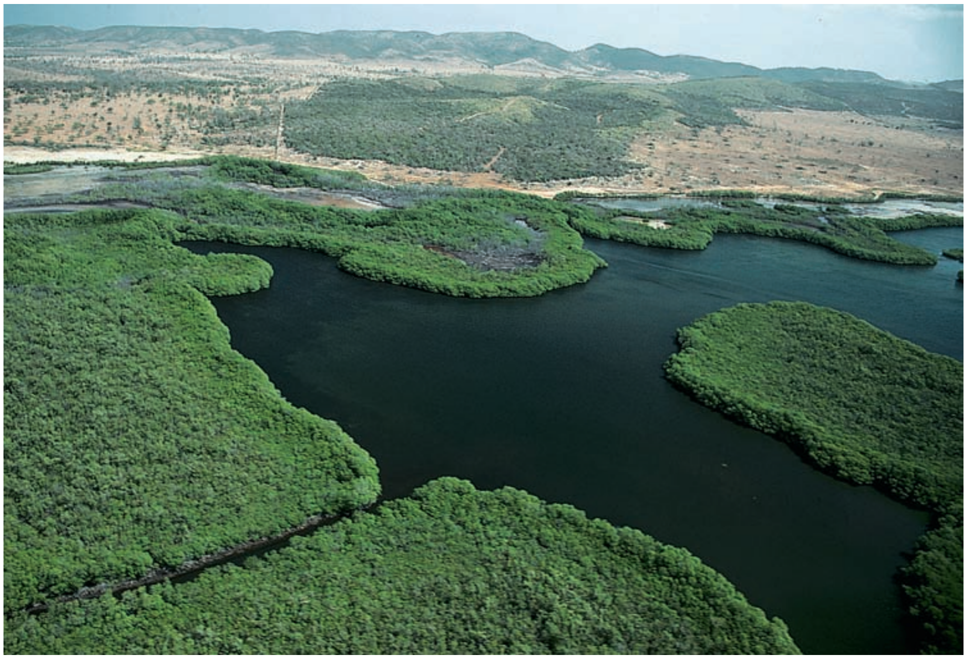


FIGURE 12.18 Aerial view of a mangrove forest on the southern coast of Puerto Rico. The outer seaward edge of the forest is dominated by the red mangrove (*Rhizophora mangle*). As in Florida and most of the Western Hemisphere, the inner margin of the red mangrove is bordered by a broad belt of black mangrove (*Avicennia germinans*). Farther away from the black mangrove is the white mangrove (*Laguncularia racemosa*).

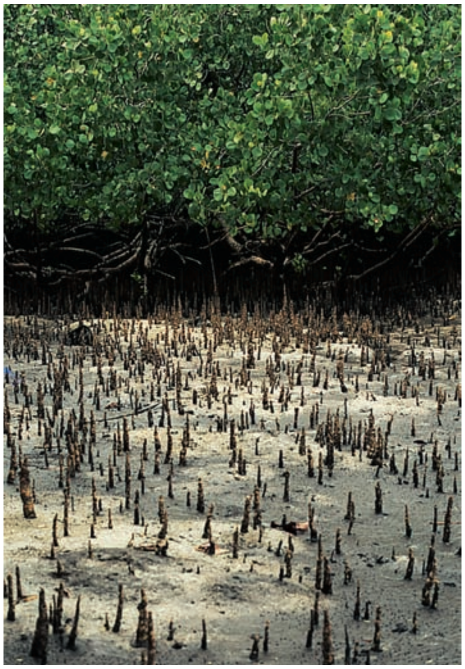


FIGURE 12.19 Pneumatophores, the vertical extensions of shallow roots, obtain additional oxygen in mangroves such as *Sonneratia alba.* Here in Palau, western Pacific, this species is found along the seaward fringe of mangrove forests.

with by far the largest number of mangrove species. Mangrove forests extend as far as 320 km (200 mi) inland in southern New Guinea and some islands in Indonesia, where the influence of the tides extend far up estuaries.

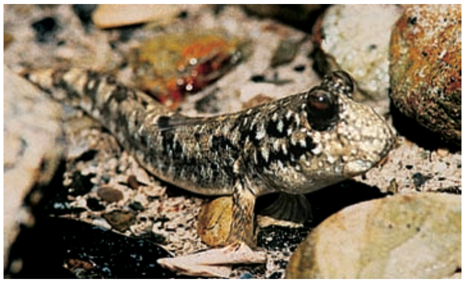
Atlantic and eastern Pacific mangrove forests, though not as extensive and diverse as those in the Indo-West Pacific region, are nevertheless of great ecological significance. The most common species of mangrove along the shores of southern Florida, the Caribbean, and the gulfs of California and Mexico is the red mangrove (*Rhizophora mangle*). It lives right on the shore (Fig. 12.18) and is easily identified by its peculiar prop roots, which branch downward and support the tree-like stilts (see Fig. 6.14). Flexible aerial roots drop down from the higher branches, helping extend the tree laterally. The trees can be as high as 9 m (30 ft). Under optimal conditions they form dense forests noted for their high primary production. Other species of *Rhizophora* are found on tropical coasts around the world.

Along the Caribbean and Atlantic coasts of the Western Hemisphere, the black mangrove (*Avicennia germinans*) and the white mangrove (*Laguncularia racemosa*) live inland from the red mangrove (Fig. 12.18). Black mangrove seedlings can survive the high salinity of the water that remains standing after high tide flooding. As a result, the black mangrove grows higher in the intertidal than the red mangrove. The black mangrove, like several Indo-West Pacific mangroves, develops **pneumatophores,** conspicuous, unbranched extensions of the shallow roots that grow upward from the oxygen-poor mud to help aerate the plant tissues (Fig. 12.19). White mangrove seedlings do not easily tolerate flooding by seawater, and as a consequence, the white mangrove is found only along the landward edge of the mangrove forest. Its leaves have two clearly visible salt glands at the base for the excretion of salts. Salts are also excreted by the leaves of the black mangrove.

Many marine and land animals live in mangrove forests. Crabs are particularly common. Many, such as species of *Sesarma* and *Cardisoma,* feed on the abundant leaf litter that accumulates below the mangrove trees. These crabs spend most of their lives on land, but when eggs are ready to hatch, females must release the larvae at sea. Several species of fiddler crabs (see "Fiddler on the Mud," p. 273) excavate burrows in the mud. As in temperate mudflats and salt marshes, burrowing crabs help oxygenate the sediment.

Mudskippers (*Periophthalmus;* Fig. 12.20) are unique fishes found in Indo-West Pacific mangrove forests and mudflats. They have burrows in the mud but spend most of their time out of the water, skipping over the mud and crawling up mangrove roots to catch insects and crabs. When out of the water, mudskippers can take oxygen from the air through blood-rich surfaces in the mouth and on the skin as long as the surfaces remain moist.

FIGURE 12.20 A mudskipper (*Periophthalmus*) from the mudflats of a mangrove forest in Papua New Guinea. Its protruding eyes are adapted to see in air. Each eye can be retracted into a moist pocket to keep it from drying out.



Many organisms attach to, or take shelter among, the submerged mangrove roots (Fig. 12.21). Large sponges living on the roots have been found to provide significant amounts of nitrogen compounds to mangrove plants. They also help protect the roots from burrowing isopods, which otherwise can cause considerable damage.

The muddy bottom around mangroves is inhabited by a variety of deposit and suspension feeders, as on mudflats. These include polychaetes, mud shrimps, and clams. The channels that cross mangrove forests are rich nurseries for many species of commercially important shrimps, spiny lobsters, and fishes. They are also nurseries for coral reef fishes. In Thailand alone, mangrove forests annually contribute an estimated \$3.5 million per km^2 (\$1.4 million per mi^2) to the economy.

Birds make their homes in the mangrove branches and feed on fishes, crabs, and other prey. Snakes, frogs, lizards, bats, and other land animals also live in the mangrove trees.

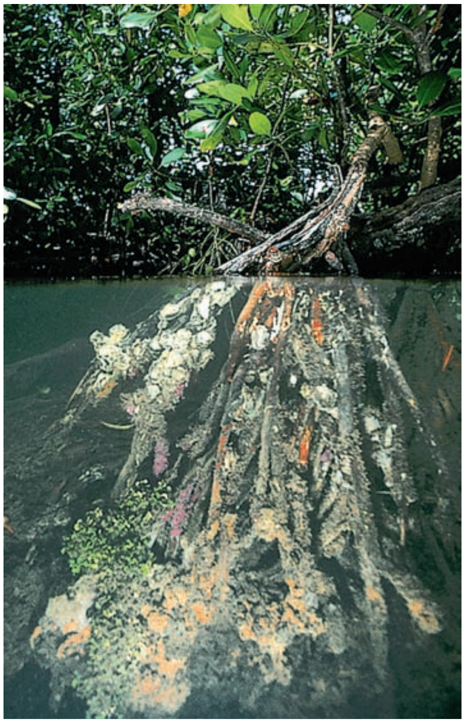


FIGURE 12.21 Seaweeds, sponges, oysters, sea anemones, barnacles, sea squirts, and many other types of organisms live attached to the roots of the red mangrove (*Rhizophora mangle*).

Large amounts of leaves and other dead plant material accumulate in the mangrove forest. Considerable amounts are eaten by crabs, and some is exported to other ecosystems. Much of the detritus, however, is broken down by bacteria. This makes the mud among the mangrove roots black and oxygen-deficient, much like that in salt marshes. Because of the oxygen-poor sediments, and toxic substances released by the leaves, life on muddy bottoms in mangrove forests is less abundant than on similar bottoms elsewhere.

Other Estuarine Communities The muddy bottoms below low tide levels are sometimes covered by beds, or meadows, of grass-like flowering plants known as **seagrasses.** They include eel grass (*Zostera;* see Fig. 6.13*b*), which is restricted to temperate waters, and turtle grass (*Thalassia;* see Fig. 6.13*d*), a warm-water species often found around mangrove forests. The roots of seagrasses help stabilize the sediment, and their leaves provide shelter to many organisms as well as being an additional source of detritus. Seagrass beds are not restricted to estuaries and are discussed in more detail in Chapter 13 (see "Seagrass Beds," p. 290).

Oysters (*Ostrea, Crassostrea*) may form extensive beds on the muddy bottoms of estuaries in temperate waters. These **oyster reefs** gradually develop as successive generations of oysters grow on the shells of their predecessors (Fig. 12.22). They provide a complex, three-dimensional surface for many organisms. The oyster-reef community includes seaweeds, sponges, tubeworms, barnacles, and other organisms that attach to the hard shells. Other animals take shelter among or even inside the shells. A similar estuarine community develops in association with mussel (*Mytilus*) beds, though the mussels require a hard substrate for attachment.

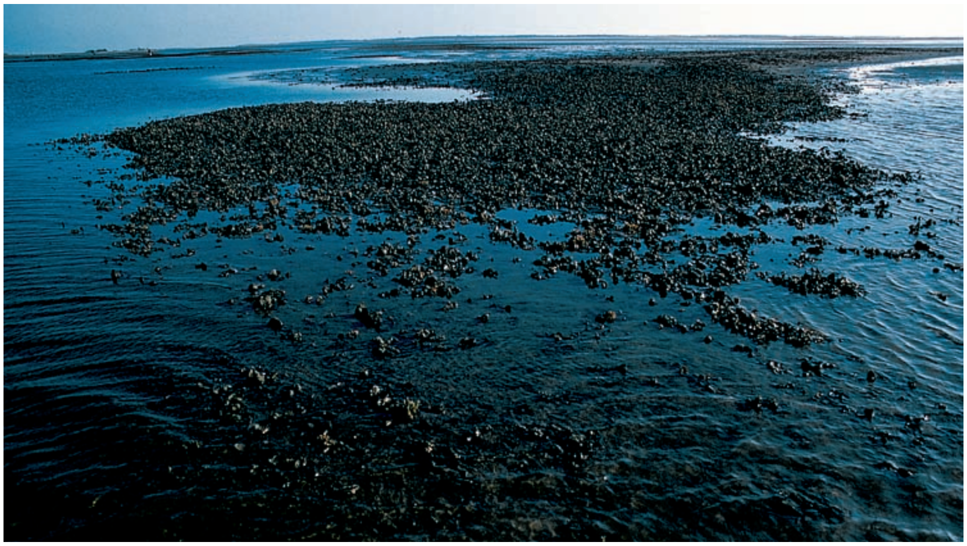


FIGURE 12.22 An oyster reef formed by the eastern oyster (*Crassostrea virginica*) on the Atlantic coast of the United States, exposed at low tide.

Feeding Interactions among Estuarine Organisms

Though relatively few species live in estuaries when compared to rocky shores, they reap the benefits of living in a very productive ecosystem. The generalized food webs shown in Figure 12.23 summarize the feeding relationships among different organisms in estuarine ecosystems.

Why do estuaries have a high primary production? There are several reasons. Nutrients brought in by the tide and rivers, together with those generated by nitrogen-fixing organisms and the decomposition of detritus, are used by plants, algae, and bacteria, the primary producers. Primary production is especially high in the communities that surround estuaries. The dense stands of cordgrass and other salt-marsh plants (or mangroves in the tropics) are particularly adapted to live on the mud and thus take advantage of the high concentration of nutrients in the sediments. The diatoms and bacteria in the mud and the phytoplankton in the water also contribute significantly to primary production.

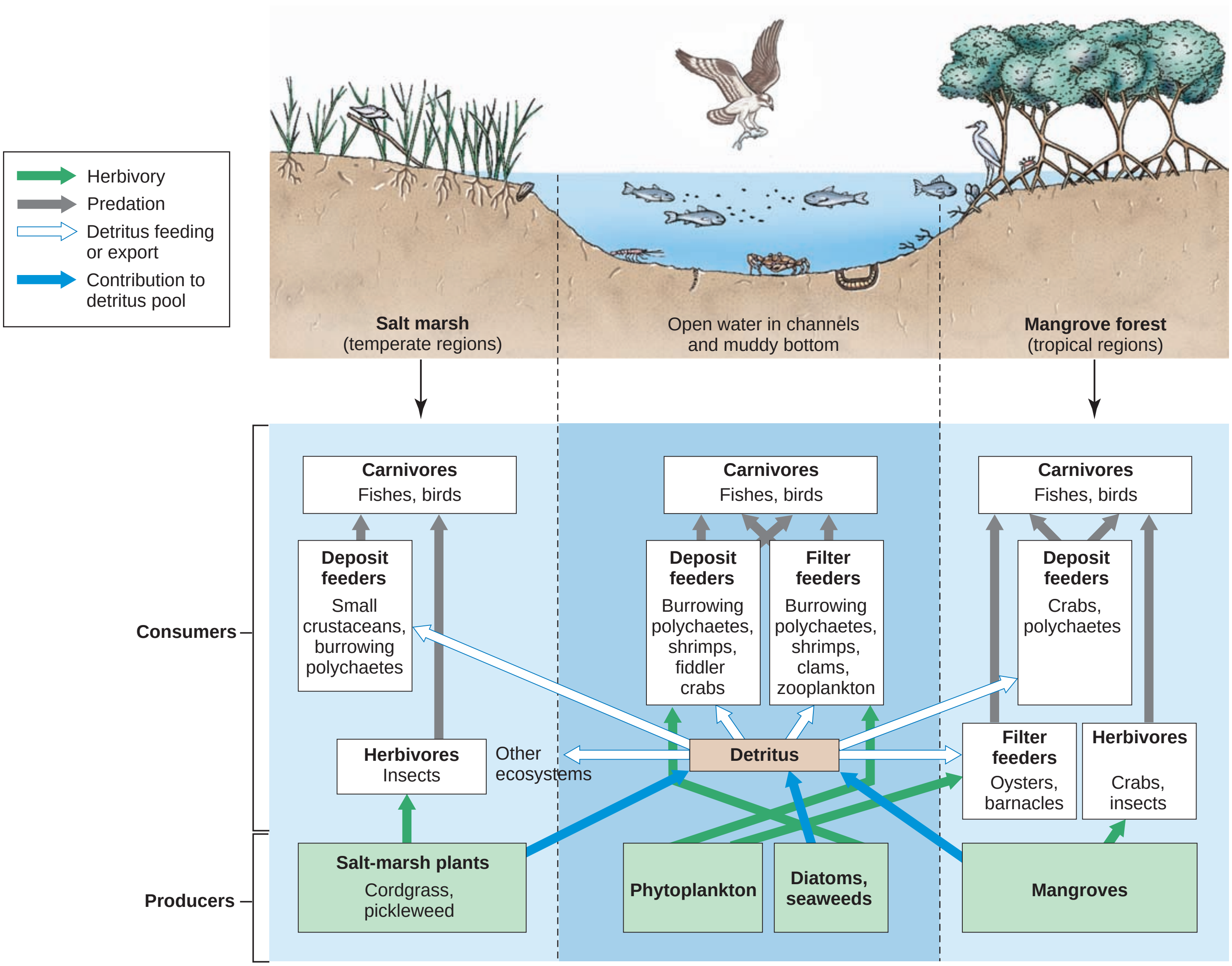

Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Salt marsh (temperate regions)
Open water in channels and muddy bottom
Mangrove forest (tropical regions)
Consumers
Producers
Carnivores Fishes, birds
Carnivores Fishes, birds
Carnivores Fishes, birds
Deposit feeders Small crustaceans, burrowing polychaetes
Deposit feeders Burrowing polychaetes, shrimps, fiddler crabs
Filter feeders Burrowing polychaetes, shrimps, clams, zooplankton
Deposit feeders Crabs, polychaetes
Herbivores Insects
Other ecosystems
Detritus
Filter feeders Oysters, barnacles
Herbivores Crabs, insects
Salt-marsh plants Cordgrass, pickleweed
Phytoplankton
Diatoms, seaweeds
Mangroves

FIGURE 12.23 Generalized food webs in estuarine ecosystems. Salt marshes (left) occur in temperate regions, mangroves (right) in the tropics.

Detritus also tends to sink to the bottom. Bottom water, which has a higher salinity and density than shallower water, thus acts as a nutrient trap in deep estuaries. Some phytoplankton are known to migrate to deep water at night to take in nutrients and move up to shallow, sunlit water the next day to carry out photosynthesis.

Primary production by estuary plants and other organisms varies geographically and seasonally, as does their relative contribution to the ecosystem as a whole. Estimates of primary production range from 130 to nearly 6,000 grams dry wt/m^2/year for cordgrasses in salt marshes on the Atlantic coast of the United States. See Table 10.1 (p. 225) for a summary of the typical rates of primary production for salt marshes, mangroves, and seagrass beds.

The organic material manufactured by primary producers is made available to consumers mainly in the form of detritus. A distinctive feature of estuarine ecosystems is that most of the animals feed on dead organic matter. Except for insects, geese, and some land animals on the fringes, relatively few herbivores actually graze on salt-marsh plants. Many detritus feeders obtain more energy from the bacteria and other decomposers in the detritus than from the dead organic matter itself. They excrete any detritus that remains undigested, however, returning it to the detritus pool. The surplus detritus is exported to the open ocean and neighboring ecosystems in a process known as **outwelling.** The exported detritus serves as a valuable source of food and nutrients to other ecosystems. The amount of exported detritus varies among estuaries, and some are actually net importers. Nonetheless, outwelling is an important role of estuaries, an additional reason that they should be preserved and protected.

Estuaries include plant-dominated communities with very high primary production. Much of the food manufactured by these plants is made available to consumers by way of detritus.

HUMAN IMPACT ON ESTUARINE COMMUNITIES

The environmental consequences of human intrusion in estuarine communities, particularly in highly productive salt marshes and mangrove forests, have been disastrous. Countless have been obliterated (see Fig. 18.1), and many surviving ones are endangered.

All around the globe estuaries are being dredged to make marinas, artificial harbors, and seaports. Others are filled to create everything from industrial parks and urban development to garbage dumps. The dredging of navigation channels increases the exposure of estuaries to wave action, which often results in the destruction of salt marshes. Another problem is the reduction or elimination of normal freshwater input when rivers are dammed or diverted. About one-third of all estuaries in the United States have disappeared altogether; close to 70% of those in California have been lost.

The same factors that threaten salt marshes are menacing mangrove forests in the tropics. Shrimp mariculture, a booming operation in Southeast Asia, South America, and other tropical and subtropical shores (see "Mariculture," p. 392), has been particularly destructive to mangrove forests. Forests have been destroyed to build the ponds to raise the shrimp. Water from the ponds, which contains large amounts of waste, excess nutrients, and uneaten food, is sometimes flushed out to sea, causing serious pollution.

Mangrove forests have also been cleared at an alarming rate to provide space for crops, urban development, roads, and garbage dumps. The growing use of mangrove wood as fuel and timber in some areas is another cause for concern. Mangrove forests once fringed around 75% of all sheltered tropical coastlines, but 35 to 50% of these mangrove forests have been destroyed. The figure is higher for the highly diverse mangrove forests of Southeast Asia. There is evidence that damage by the 2004 Indian Ocean tsunami (see "Waves That Kill," p. 58) would have not been as severe if mangrove forests had not been cleared in some of these areas.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. A proposal is made to deepen the entrance and main channel of an estuary. What do you think will happen to the salt marshes that surround the channel? What do you predict will happen to the primary production of the estuary as a whole?
2. Some of the organic material manufactured in estuarine communities is exported to other ecosystems. What type of ecosystems receive this material? How is this material transported?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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Powledge, F., 2005. Chesapeake Bay restoration. A model of what? *BioScience,* vol. 55, no. 12, December, pp. 1032–1038. Differences of opinion are putting pressure on the restoration of an important estuary.

Rapport, D. J. and W. G. Whitford, 1999. How ecosystems respond to stress. *BioScience*, vol. 49, no. 3, March, pp. 193–203. An estuary is compared to two terrestrial ecosystems, all three of which are impacted by humans.

Step, D., 2002. Living on the edge. *Audubon,* vol. 104, no. 2, September, pp. 62–77. The preservation of estuaries and other coastal wetlands is crucial for the survival of many shorebirds.

Warne, K., 2007. Forests of the tide. *National Geographic,* vol. 211, no. 2, February, pp. 132–151. Mangrove forests provide nutrients and habitats to marine life as well as resources to millions of people.

Williams, T., 2006. The last line of defense. *Audubon,* vol. 108, no. 3, May/June, pp. 56–59, 66–71. The human impact on the coastal wetlands of the northern Gulf of Mexico is in part responsible for damage due to Hurricane Katrina.

In Depth

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Minchinton, T. E., J. C. Simpson, and M. D. Bertness, 2006. Mechanisms of exclusion of native coastal marsh plants by an invasive grass. *Journal of Ecology,* vol. 94, pp. 342–354.

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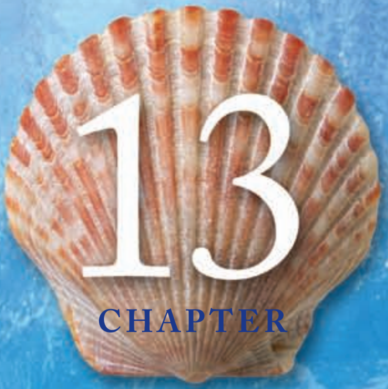
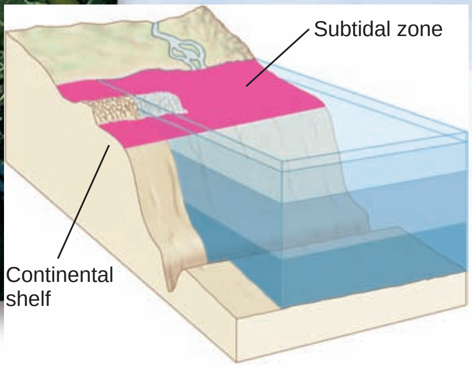
Ecklonia kelp forest, New Zealand.



13

CHAPTER

Life on the Continental Shelf



The submerged edge of the continents, the **continental shelf,** was once considered the beginning of the unknown blue sea. But when the shelf came under scrutiny during the 1800s, the unknown began to give up its secrets. We have learned even more because the use of scuba and underwater habitats has allowed firsthand study and observation (Fig. 13.1). Biologically, the shelf is the richest part of the ocean. It includes the world's most important fishing grounds, which yield about 90% of the total global catch. Oil and minerals have been found on the shelf, and nations have extended their international borders to protect their newfound, or yet-to-be found, resources. The continental shelf, being close to shore, is also profoundly affected by pollution and other activities of humans on land.

This chapter looks at life on the continental shelf, paying particular attention to the bottom organisms. Life in the water column above the shelf is discussed in Chapter 15, and the shelf's fisheries in Chapter 17. Coral reefs, many of which are found on the shelf, are covered separately in Chapter 14.

PHYSICAL CHARACTERISTICS OF THE SUBTIDAL ENVIRONMENT

The part of the continental shelf that is never exposed at low tide constitutes the **subtidal zone** of the marine environment. The subtidal zone, which is sometimes called the **sublittoral zone,** extends from the low tide level on shore to the **shelf break,** the outer edge of the continental shelf (see Fig. 10.12). The depth

FIGURE 13.1 Scuba diving has dramatically expanded the possibilities for the study of the subtidal environment by marine biologists.

of the shelf break varies, but it averages around 150 m (490 ft). The width of the shelf is also highly variable. It ranges from less than 1 km (0.6 mi) to over 750 km (470 mi), with an average of approximately 80 km (48 mi). The **benthos** of the continental shelf live in the subtidal zone, whereas the **plankton** and **nekton** of the water column over it inhabit the **neritic zone.**

The subtidal zone consists of the bottom of the ocean from the low tide level to the shelf break, the outer edge of the continental shelf.

The physical factors that affect subtidal organisms are linked to two of the shelf's fundamental characteristics: its relatively shallow water and its proximity to land. Because the bottom is shallow, temperature varies more from place to place in the subtidal zone than on the deeper bottom beyond the shelf. This is significant because temperature is one of the most important factors influencing the distribution of marine organisms. The kinds of organisms found in the subtidal change dramatically from the Equator to the poles. There are also *more,* not just different, species in the tropics than in temperate or polar waters. The bottom below the Arctic and Antarctic ice, however, is far from being a desert (see "Under the Antarctic Ice," p. 286).

The bottom in shallow water is also much more affected by waves and currents than in deep water. The rise and fall of tides can produce particularly strong **tidal currents** on the shelf, especially in bays and narrow straits. Wind waves can affect the bottom even at depths of 200 m (650 ft). Water motion, or **turbulence,** stirs up the water column and prevents **stratification.** Thus, except for seasonal or short-term variations, the temperature and salinity of the water at the bottom of the subtidal are not much different from those at the surface. More importantly, nutrients do not concentrate in the bottom layer and become unavailable to primary producers at the surface, as they do in deep water (see "Nutrients," p. 346). Nutrients are also brought in by rivers, sometimes as by-products of the highly productive salt marshes or mangrove forests that fringe the shore. As a result, the water over the continental shelf is far more productive and plankton-rich than the open ocean, so much more food is available. The high concentration of phytoplankton, plus decaying organic matter brought in by rivers, gives coastal water a greenish tint as opposed to the deep blue of open-ocean water.

Rivers, obviously, also bring in large amounts of fresh water. Freshwater runoff dilutes the seawater, reducing its salinity. The effects of large rivers such as the Mississippi and the Amazon extend many miles offshore. Away from the influence of rivers, however, the salinity of coastal water is about the same as that beyond the shelf.

The combination of proximity to land and shallow water greatly influences **sedimentation,** the settling of sediment particles from the water. Most of the sediment on the shelf is **lithogenous,** and rivers bring in huge quantities of sediment from the continents. Water motion sorts out the particles by size and density, especially on the shallower parts of the shelf. Large-grained material such as gravel and sand settles out even in areas with strong waves and currents. On the other hand, turbulence keeps fine particles such as silt and clay in suspension. Fine particles are deposited only in quiet areas or in deeper water when turbulence does not reach the bottom.

The abundant phytoplankton plus the sediment that is brought in by rivers and stirred up by waves and currents make shelf water murkier than that in the open ocean. Light does not penetrate as deeply, which reduces the depth at which primary producers—phytoplankton and attached seaweeds and seagrasses—can carry out photosynthesis and grow.

The type of substrate, depth, turbulence, temperature, salinity, and light are among the most important physical factors that influence life on the continental shelf.

CONTINENTAL SHELF BOTTOM COMMUNITIES

The type of substrate is very important in determining which particular organisms inhabit the floor of the continental shelf. It also dictates how they are sampled by marine biologists (Fig. 13.2). In fact, subtidal communities are often classified according to the type

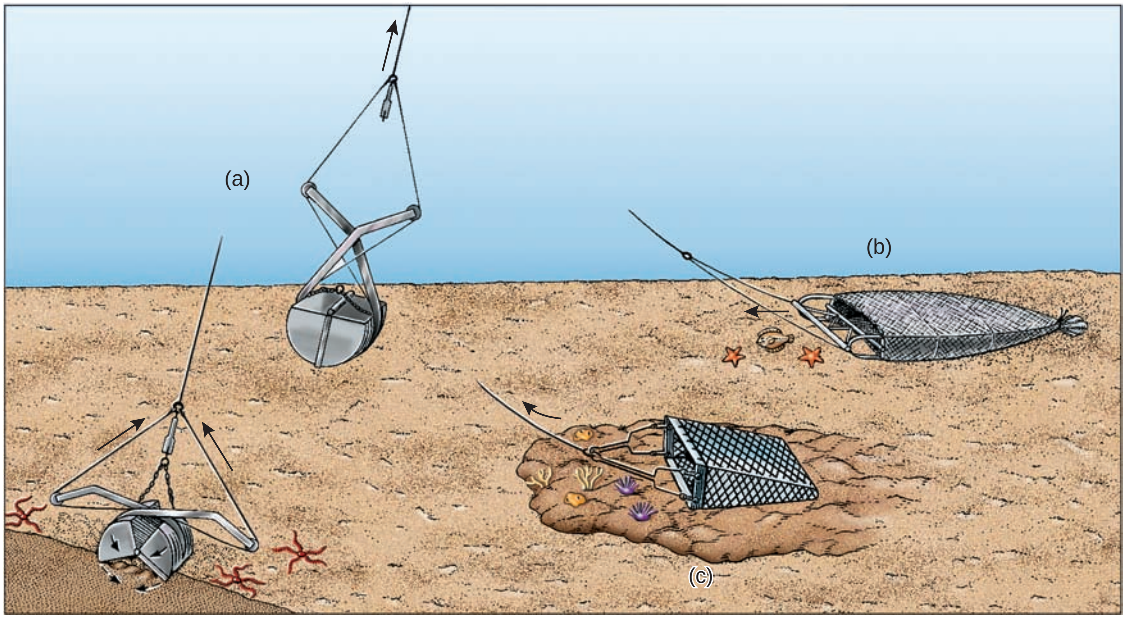


FIGURE 13.2 Though scuba diving is an excellent method for sampling and studying subtidal environments, its use is limited to shallow depths. Soft bottoms at greater depths can be studied by using various sampling gears. *Bottom grabs* (*a*) such as the Van Veen grab are lowered from the surface. The jaws close, grabbing a sample of bottom sediment, as the dredge is retrieved. Different types of *bottom trawls* (*b*) are used to collect the larger inhabitants of soft bottoms. They are similar to the bottom trawls used by fishers (see Fig. 17.6*d*). *Dredges* (*c*) with heavy metal frames are used to scrape organisms off rocky bottoms.

of substrate. The most common of these are communities associated with soft bottoms. Hard-bottom, or rocky-bottom, communities constitute the second type.

Soft-Bottom Subtidal Communities

Sandy and muddy substrates dominate the world's continental shelves. Large areas covered by soft sediments stretch from the shore to the edge of the shelf. Even along rocky shores, rocks eventually give way to sand or mud in deeper water. The organisms that inhabit these often flat and seemingly homogeneous bottoms (Fig. 13.3) are not necessarily distributed by chance. It has long been recognized that these organisms form distinct communities whose distribution is greatly influenced by such factors as the particle size and stability of the sediment, light, and temperature.

The shelf's soft-bottom communities share many traits with the communities of sandy beaches and mudflats covered in Chapters 11 and 12. **Infauna,** animals that burrow or dig in the sediment, predominate in all these communities. There are also, however, some **epifauna,** animals that live on top of the sediment. Because the soft bottom offers nothing to hold on to, **sessile,** or attached, forms are rare.

Most of the continental shelf is covered by mud or sand. The subtidal communities in these areas are dominated by infauna.

The number of species living on subtidal soft bottoms is usually higher than the number of species on soft bottoms in the intertidal zone. This is largely because of the relatively more stable physical conditions below the low tide mark. Desiccation is not a problem. Furthermore, there are none of the drastic temperature changes caused by exposure at low tide or the salinity variations of estuarine mudflats.

The close relationship between particle size and the distribution of organisms is particularly evident in the infauna, which for the most part are very selective as to where they live. Different species may also partition their environment and thus reduce competition by living at different depths in the substrate. Because only the upper layer of sediment contains enough oxygen, however, the depth at which the infauna can live is limited. In organic-rich mud, oxygen is quickly used up by decomposition. In contrast, sand usually contains less organic matter. It

Benthos Organisms that live on the bottom.
Plankton Those that drift with the currents.
Nekton Those able to swim against the currents.
- Chapter 10, p. 220; Figure 10.11

Stratification Separation of the water column into layers, with the densest, coldest water at the bottom, which prevents the mixing of the nutrient-rich deep water with the less dense, warmer upper layer.
- Chapter 3, p. 53; Figure 3.22

Lithogenous Sediment Sediment that comes from the physical or chemical breakdown of rocks on land.
Biogenous Sediment Sediment composed of the skeletons and shells of marine organisms.
- Chapter 2, p. 32

Under the Antarctic Ice

Antarctica, one of the last unspoiled wildernesses on earth, is for many of us a vision of awesome whales, smiling seals, and frolicking penguins. Life on the Antarctic shelf is as fascinating and pristine as in the cold waters above it.

Ice is a major physical factor for shelf organisms in the Antarctic. A layer of ice several meters thick forms during winter, freezing and eventually crushing any organisms living on the bottom. Winds and currents push the ice, scouring the bottom and crushing even more organisms. Ice may also form around the organisms to depths of 30 m (100 ft) or more. The ice, less dense than the water, often floats to the surface, carrying with it these trapped, often frozen, organisms. Except for these effects of winter ice at shallow depths, however, the physical environment in Antarctic waters is remarkably constant. Year-round low temperatures mean that life processes, including growth, proceed at a slow pace. In contrast to the Arctic region, there is no runoff from rivers in Antarctica. Another important difference from the Arctic is the absence of disturbance from the feeding of large mammals such as the gray whale and the walrus in Antarctica.

Though kelps are present on several of the offshore islands, they are surprisingly absent in mainland Antarctica. Here they are replaced by *Desmarestia* and a few other brown seaweeds. These are not considered kelps, though they may be large.

Sessile organisms are rare at the shelf's shallower depths because of the scouring effect of winter ice. Below this depth, however, benthic invertebrates are plentiful. The invertebrate fauna of Antarctica is rich, colorful, and highly diverse. Many of the invertebrate species are unique to the continent. They evolved there over a long period of isolation from the continental shelves of other continents.

The nutrient-rich waters result in very high primary production when sunlight becomes available during the long days of summer. Rich blooms of phytoplankton (diatoms even grow in the ice) provide food for the many suspension feeders. Sponges in particular are so common that they cover most of the bottom in many places.

Sponges are represented not only by many different species but also by a multitude of growth forms. Huge, volcano-like sponges may grow 2 m (close to 7 ft) or more in height. These large individuals are probably hundreds of years old. Others are fan-shaped or resemble bushes or branching corals. These and other sponges provide refuge and perches for many fishes and other mobile animals, much as kelps or corals do elsewhere. Sponges are so common that the bottom below 30 m (100 ft) or so is nothing but a thick mat of siliceous, or glass, sponge spicules—truly a glass bottom.

Glass spicules may play an amazing role in some Antarctic sponges that harbor symbiotic algae. The green algae may provide some nutrients to the sponges but must obtain light in order to carry out photosynthesis. How these symbiotic algae survive deep inside sponges that live in water covered by a thick sheet of ice is something that puzzles marine biologists. The answer seems to be in the glass spicules. They efficiently transmit to the algae what little light reaches the sponges, a real network of fiber-optic cables!

Other invertebrates abound: sea anemones, soft corals, sea stars, nudibranchs, and sea urchins. Many of these, like sponges, are suspension feeders, while others feed on the sponges. To protect themselves against predators, many sponges produce toxic substances. These chemical defenses are especially common in those sponges with bright colors. Others are predators of sponge feeders and help keep the slow-growing sponges from being wiped out. Not all of these subtidal invertebrates are unique to Antarctica. Some are found elsewhere, but in progressively deeper water as one gets closer to the Equator.

A tree-like soft coral, a yellow sponge, scallops, and other benthic invertebrates from Antarctica.

Antarctic fishes are remarkable in their own right because they can remain active at temperatures that are close to the freezing point of seawater. Many have a chemical "antifreeze" in their blood. The cold water holds so much dissolved oxygen that some, like icefishes, have colorless blood that lacks hemoglobin.

The wonders of life in Antarctica, both below and above the ice, are unfortunately being threatened. The Antarctic Treaty, signed by 45 nations to administer and manage the continent, now forces polluters to repair damage that they cause or be fined. Cruise-ship tourists, fishing vessels, oil and sewage pollution, leftover garbage, the potential exploitation of oil and mineral resources, and an ozone hole over the continent (see "The No-Zone," p. 238) could eventually overwhelm our most desolate continent and harm its unique life.

is also more porous, so water can circulate through the sediment and replenish the oxygen (see Fig. 11.28). Thus, the infauna can burrow deeper in sand than in mud. Even in mud, however, the presence of burrows aids circulation, helping organisms obtain oxygen.

Soft substrates often contain patches of different types of sediment. As a result, the distribution of organisms along the bottom is typically **patchy,** that is, the organisms occur in distinct clumps or patches (Fig. 13.4). Some species have a patchy distribution because their planktonic larvae select a particular environment on which to settle and undergo **metamorphosis.** Some larvae are known to postpone metamorphosis and "taste" the bottom until they find a certain type of substrate (see "Larval Ecology," p. 219). Metamorphosis may be triggered by specific chemical, physical, and biological factors (Fig. 13.5). The larvae of some species can sense adults and prefer to settle near them. This may cause the species to be distributed in clumps even if there is a uniform bottom. The arrival of new individuals to a population, either by settling larvae or by migrating juveniles or adults, is known as **recruitment**.

Unvegetated Soft-Bottom Communities The great majority of the shelf's soft-bottom communities lack significant

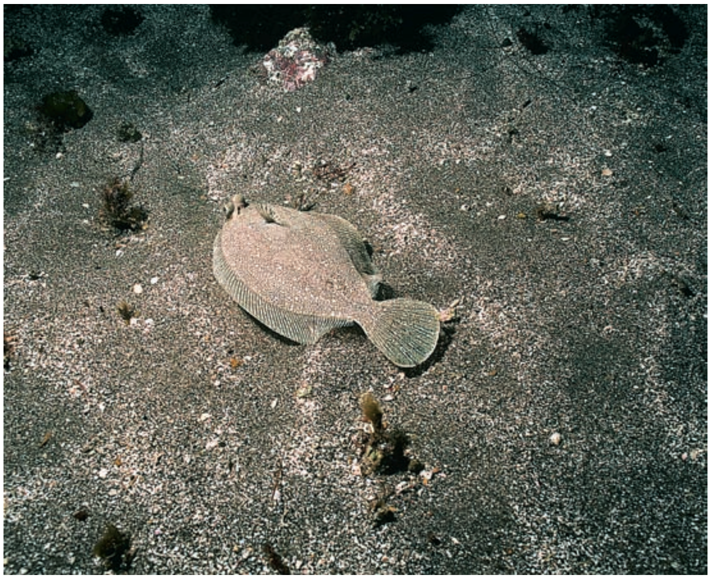
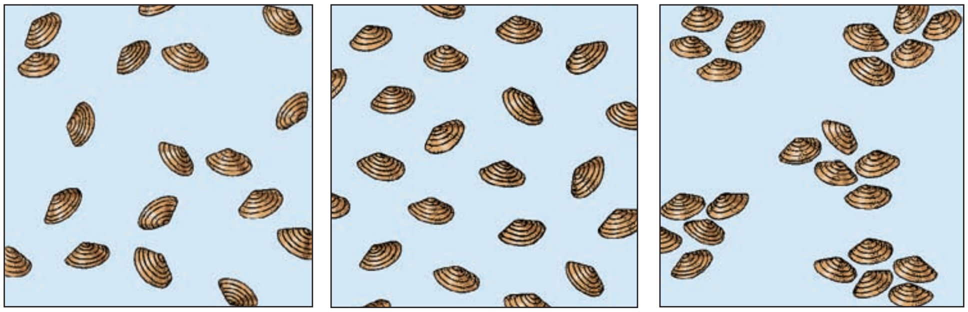


FIGURE 13.3 Conspicuous life on shallow sandy bottoms includes occasional clumps of seaweeds that manage to grow on small rocks or shells and large predators like flatfishes.



(a) Random (b) Regular (c) Patchy

FIGURE 13.4 The spacing, or distribution, of organisms can be classified into three basic types: (*a*) *random,* in which animals are scattered with no particular pattern, (*b*) *regular,* where they are spaced at even intervals, and (*c*) *patchy,* or *clumped,* where they cluster together. Many marine species show a patchy distribution. Can you think of a reason organisms such as clams might show a regular distribution?

amounts of seaweeds or seagrasses. They are therefore known as **unvegetated** communities. The absence of large seaweeds and plants is the defining feature of these communities. Sea lettuce (*Ulva*) and other green algae such as *Enteromorpha* may grow in the shallows, but only on hard surfaces such as rocks and shell fragments. The main primary producers are diatoms and a few other microscopic algae and bacteria that grow on sand or mud particles in shallow water. This almost complete absence of seaweeds and plants means that, as on sandy beaches, primary production by benthic **primary producers** is usually very low. Nearly all primary production is by phytoplankton that are not part of the bottom communities.

Because there is little primary production by benthic organisms, **detritus** is a very important food source for many inhabitants. Detritus is brought in by currents from estuaries, rocky shores, and other, more productive coastal communities. It is also present as feces, dead individuals, and other debris from the plankton and nekton in the water column. Detritus is also generated by the bottom inhabitants themselves.

The detritus is used by bacteria and by the many types of microscopic animals that live between the sediment particles, the **interstitial** animals, or **meiofauna** (see "Life in Mud and Sand," p. 291).

Larger benthic invertebrates also feed on detritus. They are mostly burrowing **deposit feeders** (Fig. 13.6). Polychaetes are the most diverse group of deposit feeders in the soft sediments of the shelf. Trumpet (*Pectinaria;* Fig. 13.6) and bamboo worms (*Clymenella;* see Fig. 12.11) are deposit-feeding polychaetes that inhabit tubes they build from sediment particles. Lugworms (*Arenicola*) and others live in burrows. These polychaetes and other worms eat detritus and other organic matter by collecting it with their tentacles or by ingesting sediment and extracting food from it.

Some sea urchins are uniquely adapted to living as deposit feeders on soft bottoms. Heart urchins (*Spatangus*) have abandoned the round shape of most urchins, becoming more streamlined with shorter spines that lie flat (Figs. 13.6 and 13.7). Sand dollars (*Dendraster*) are almost completely flat and have very short spines (Figs. 13.8 and 7.47*b*). They typically feed on detritus and use mucus to carry particles to the mouth. Other deposit feeders among the infauna include echiurans (Fig. 13.9), peanut worms, sea cucumbers, and ghost shrimps (*Neotrypaea;* see Fig. 12.11).

The infauna also include **suspension feeders** that eat drifting detritus and plankton from the water column. Many of these suspension feeders are **filter feeders** and actively filter the water to obtain suspended particles. Soft-bottom suspension feeders include many types of clams (Fig. 13.6): razor clams, the quahog (*Mercenaria mercenaria*), cockles, the soft-shelled clam (*Mya arenaria*), and others. Most clams are filter feeders, but some—such as the bent-nosed, or small, clams and the file yoldia—are deposit feeders. They collect

Metamorphosis The transformation of onestage of a life cycle into another, as when a larva changes into a juvenile.
- Chapter 7, p. 117

Primary Producers Organisms that can create organic matter from CO_2, usually by photosynthesis.
- Chapter 4, p. 68

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

Deposit Feeders Animals that feed on organic matter that settles in the sediment.
Suspension Feeders Animals, including *filter feeders*, that feed on particles suspended in the water column.
- Chapter 7, p. 116; Figure 7.3

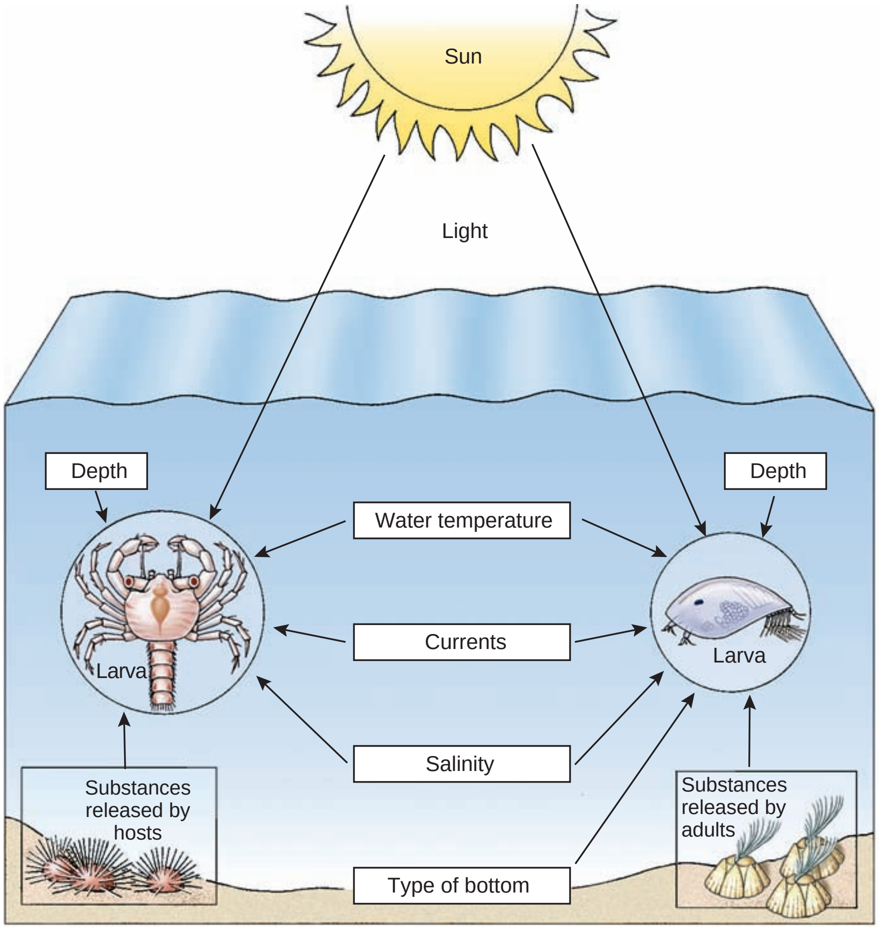

Sun
Light
Depth
Depth
Water temperature
Currents
Salinity
Type of bottom
Larva
Larva
Substances released by hosts
Substances released by adults

FIGURE 13.5 Many factors are known to influence the settlement and metamorphosis of planktonic larvae. The larva illustrated on the left, a megalopa (see Fig. 7.39), belongs to a crab (*Echinoecus pentagonus*) that as an adult lives on tropical sea urchins. The larva on the right is the cypris larva of a barnacle. Many barnacle larvae settle near adults of their species.

detritus and microscopic organisms with their siphons or specialized appendages (Fig. 13.10). Also among the filter feeders are some amphipods (Fig. 13.6) and polychaetes such as parchment worms (Fig. 13.6) and terebellids (Fig. 13.11).

The distribution of burrowing deposit and suspension feeders is influenced by several factors. Already mentioned in the previous section is the type of substrate. Deposit feeders tend to predominate in muddy sediments because more detritus settles in areas of low turbulence and is ultimately retained in the smaller interstitial spaces between mud particles (Fig. 13.12). Suspension feeders, on the other hand, are more common on sandy bottoms. Suspension feeders such as sea pens (*Stylatula;* Fig. 13.13) and sea pansies (*Renilla*) can often be found in dense stands.

The types of organisms present also affect the establishment of others. Deposit feeders, for instance, are known to exclude suspension feeders (see “Mudflats,” p. 270). Some deposit feeders and other members of the infauna are known as **bioturbators** because they move sediment while burrowing or feeding. They uncover and oxygenate deeper sediments and bury those on the surface. Sea cucumbers (see Fig. 11.32), echiurans (Fig. 13.9), peanut worms, some fishes, and even whales are important bioturbators.

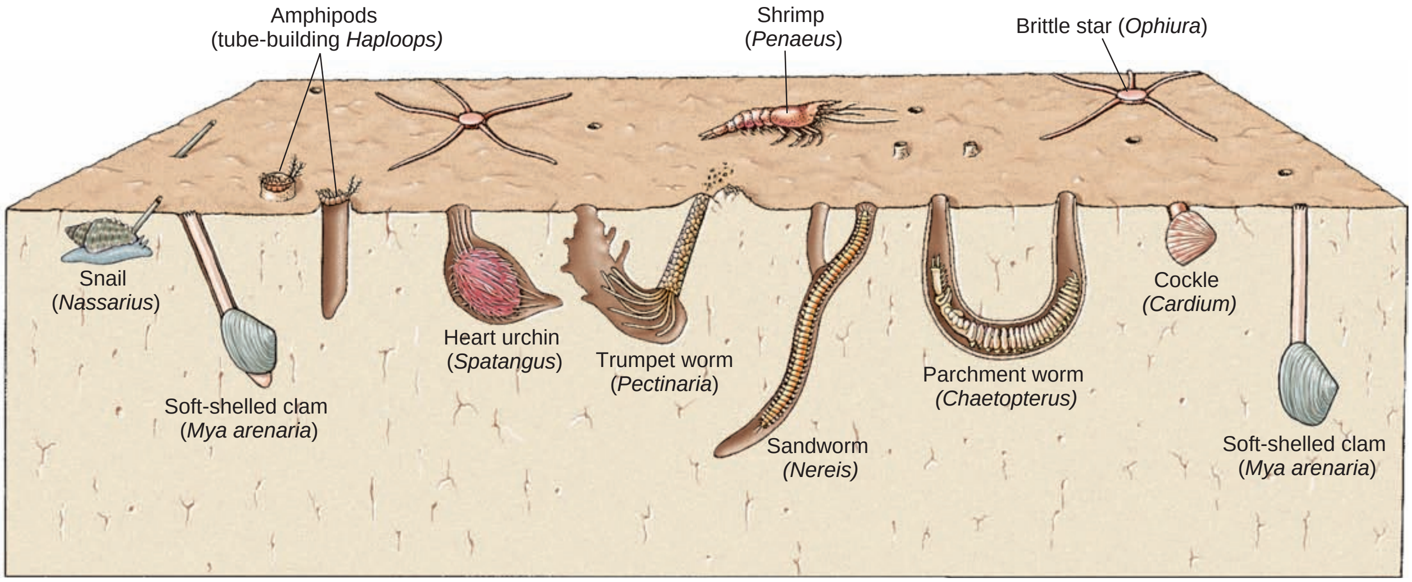

Amphipods (tube-building *Haploops)*
Shrimp (*Penaeus*)
Brittle star (*Ophiura*)
Snail (*Nassarius*)
Soft-shelled clam (*Mya arenaria*)
Heart urchin (*Spatangus*)
Trumpet worm (*Pectinaria*)
Sandworm *(Nereis)*
Parchment worm *(Chaetopterus)*
Cockle *(Cardium)*
Soft-shelled clam (*Mya arenaria*)

FIGURE 13.6 Representatives of the infauna and epifauna of subtidal soft bottoms in different parts of the world. Also see Figure 12.11 for a sample of mudflat inhabitants.

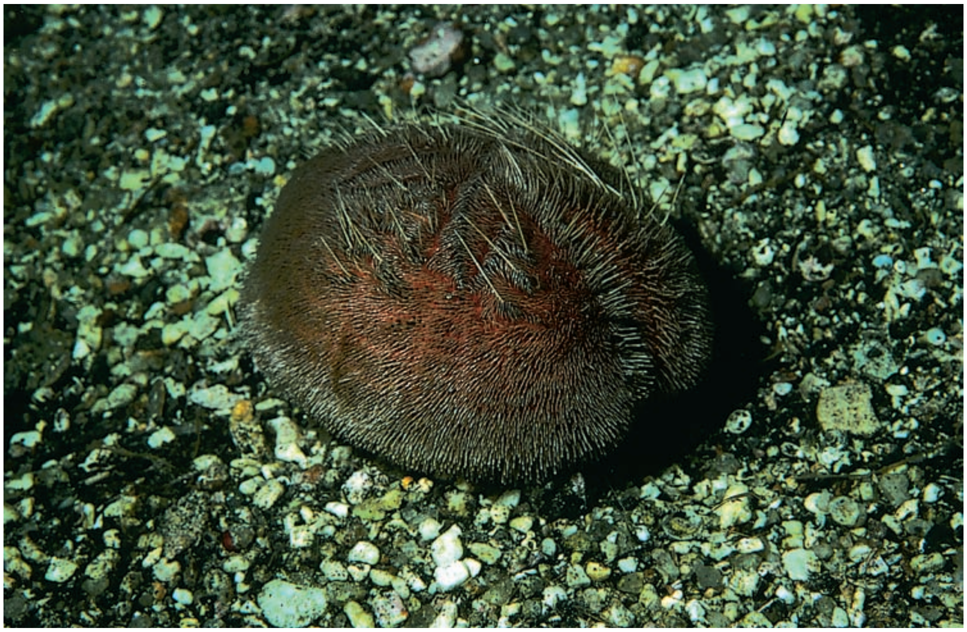


FIGURE 13.7 Like all heart urchins, *Spatangus purpureus* is specialized for living in sediments. Heart urchins burrow below the surface (see Fig. 13.6) and use modified tube feet for feeding. This photo was taken in the Mediterranean Sea at night, when the urchin emerged from the sediment.

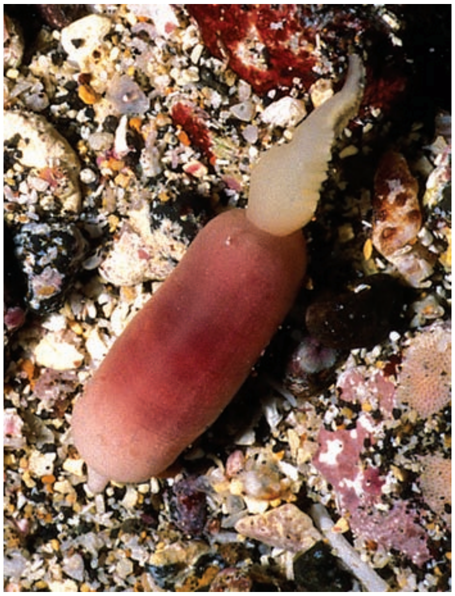


FIGURE 13.9 *Thalassema steinbecki* is a deposit-feeding echiuran that inhabits soft bottoms along the Pacific coast of North and South America from Baja California to the Galápagos Islands.

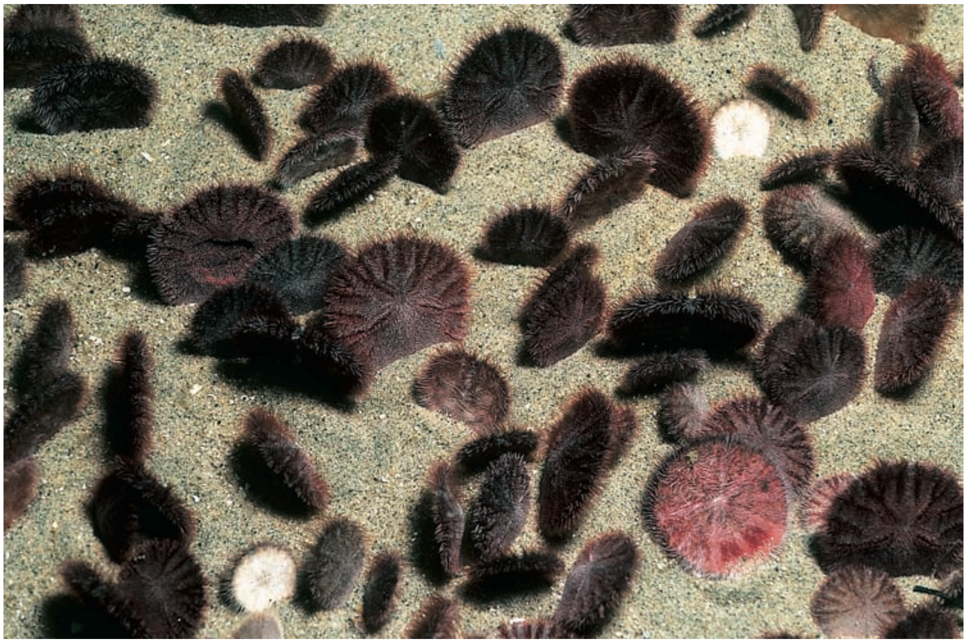


FIGURE 13.8 These sand dollars (*Dendraster excentricus*) form dense beds on sandy bottoms along the California coast. They lie partially buried in the sand, angled into the current.

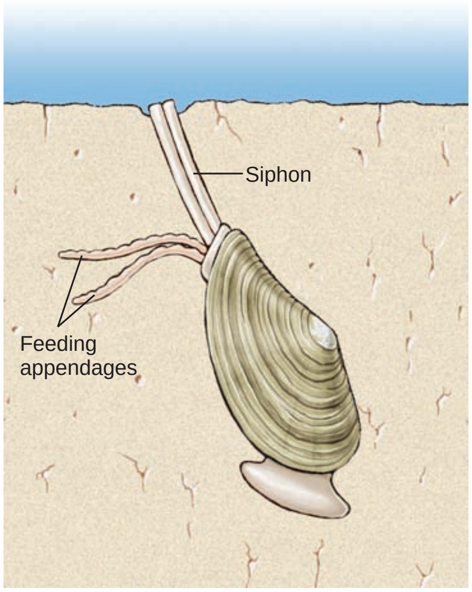


FIGURE 13.10 The file yoldia (*Yoldia limatula*) inhabits mud and muddy sand from shallow water to depths of 30 m (100 ft) in the North Atlantic. The siphon brings water in but is not used for feeding as in most other clams. Instead, this clam uses two grooved, tentacle-like appendages to feed. Each groove contains cilia that bring small organisms to the mouth.

Many tube builders are deposit feeders, but they help stabilize the substrate, making it more suitable for suspension feeders. Their tubes may also interfere with the activities of burrowing deposit feeders. The tubes slow down the flow of water over the sediment, which decreases the rate of particle suspension. The modification of the environment by deposit feeders, especially of bioturbators, and the effects of tubes are examples of how some species can indirectly influence the recruitment and survival of others.

Many epifaunal invertebrates are deposit feeders. These include most amphipods and other small crustaceans as well as many species of brittle stars (see Fig. 13.6). Most of these brittle stars use their tube feet to collect detritus from the bottom. Other brittle stars are suspension feeders that raise their arms up into

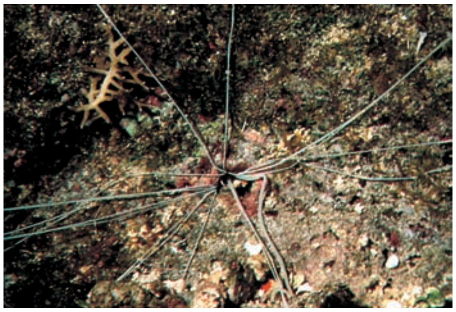


FIGURE 13.11 *Terebella* is a polychaete worm that burrows in soft bottoms or lives on hard bottoms. Its long tentacles are extended over the bottom for suspension feeding.

the water to catch suspended particles with their tube feet. Still others are **scavengers** and feed on dead animals. Shrimps, including commercially valuable species (*Penaeus*), are another type of epifaunal scavenger.

Most soft-bottom subtidal communities lack large seaweeds and plants. They are mostly inhabited by deposit and suspension feeders.

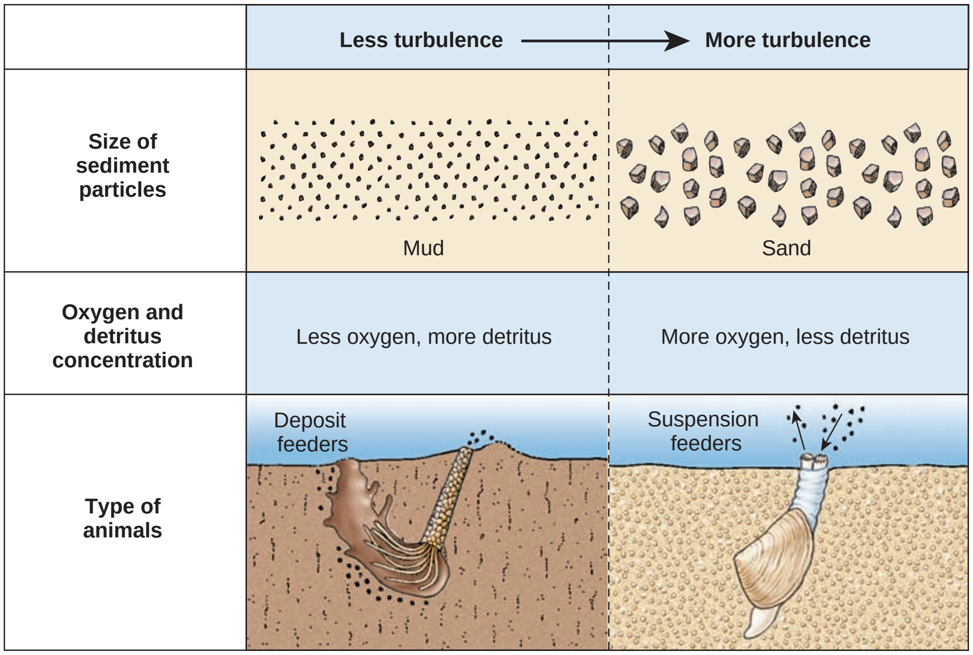

Less turbulence
More turbulence
Size of sediment particles
Mud
Sand
Oxygen and detritus concentration
Less oxygen, more detritus
More oxygen, less detritus
Type of animals
Deposit feeders
Suspension feeders

FIGURE 13.12 The distribution of suspension and deposit feeders in soft bottoms is largely influenced by the size of the sediment particles. This relationship, however, is not clear-cut. Animals already established in the sediment, for instance, influence colonization by others.

Some members of the soft-bottom epifauna are predators. They may burrow through the sediment to get their prey or catch it on the surface. As in other communities, predators are important in regulating the number and type of bottom inhabitants. They remove individuals and cause disturbances in the sediment that allow recolonization by different types of organisms. Snails such as whelks (*Nassarius;* see Fig. 13.6) and moon snails (*Polinices;* see Fig. 12.11) feed on clams by drilling a hole in the shell and rasping away the flesh. Sea stars (*Astropecten;* Fig. 13.14) prey on clams, brittle stars, polychaetes, and other animals. Predatory amphipods influence subtidal communities by preying on the settling larvae of other species. Crabs are common predators and scavengers on soft bottoms. Examples are the blue crab (*Callinectes sapidus*) and other swimming crabs, the lady crab (*Ovalipes ocellatus*), and many others that partially bury themselves in the sand or mud. Other predatory crabs, hermit crabs, lobsters, and octopuses take shelter on rocky bottoms but move to soft bottoms to feed.

Many fishes are common predators. Most bottom-dwelling, or **demersal,** fishes in these soft-bottom communities are carnivores. Rays and skates scoop up clams, crabs, and other infauna and epifauna. Flatfishes such as flounders, halibuts, soles, and turbots lie camouflaged or covered on the bottom and forage for a wide variety of prey. **Pelagic** fishes and squids also feed on the inhabitants of the shelf's soft bottoms. Some fishes only nip off the siphons of molluscs instead of eating the entire animal. A very large predator indeed is the gray whale (*Eschrichtius robustus*), which filters the sediment for amphipods and other small animals (see Fig. 9.18*b*). Large predators such as whales, walruses, and rays have important effects on soft-bottom communities. They not only remove their prey but also are bioturbators that dig pits in the bottom while feeding, killing large numbers of infauna that aren't eaten and changing the characteristics of the sediment.

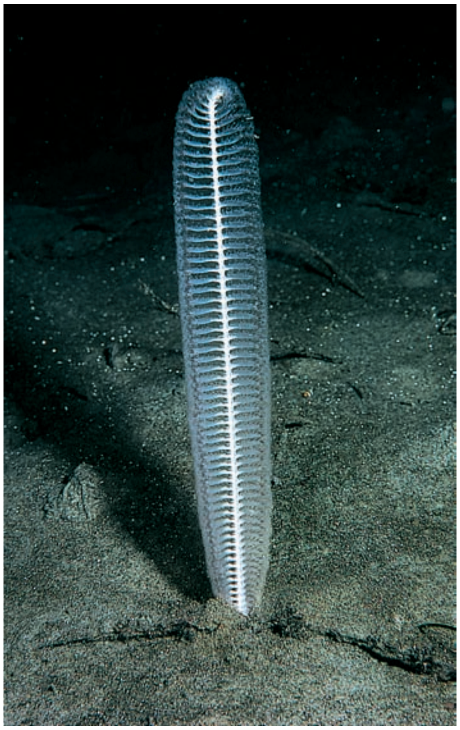
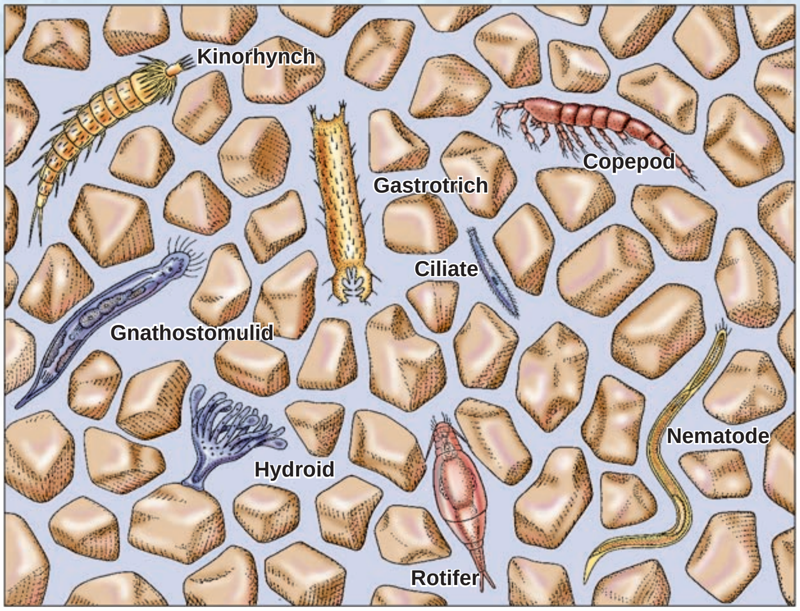


FIGURE 13.13 Sea pens are suspension-feeding cnidarians. Each individual is a colony that includes numerous minute polyps and a fleshy stalk that is anchored in soft substrates. This is *Stylatula elongata* from the Pacific coast of North America.

Seagrass Beds Soft bottoms along the coast are occasionally carpeted by **seagrasses.** These flowering plants, grass-like in appearance but unrelated to true grasses, have become established in the marine environment (see "Flowering Plants," p. 110). Seagrass beds develop best in sheltered, shallow water. They are also found in estuaries and in association with mangrove forests (see "Other Estuarine Communities," p. 279).

Only 50 to 60 species of seagrasses are known. Most are tropical and subtropical, but several species are common in colder waters. Most seagrasses are restricted to muddy and sandy areas in the subtidal zone. Some are intertidal living on rocky shores. Different species of seagrasses vary in maximum depth, but all are limited by the penetration of light through the water column.

Life in Mud and Sand



Examples of the meiofauna in sand.

The space between sediment particles is largely invisible to us, but it is an important part of the marine environment. This microscopic world, which extends from sandy beaches and estuaries to deep water, is inhabited by highly specialized **interstitial** organisms, often called the **meiofauna.**

The meiofauna are adapted to their unique environment in several ways. Their shape is typically slender and worm-like, which evolved for efficient movement between sediment particles and to increase surface area for better uptake not only of oxygen (which tends to be deficient in sediments) but also perhaps of dissolved organic matter (DOM). Some meiofauna glide freely among the sediment particles, whereas others attach to them. Though detritus is probably an important source of food, many meiofauna are predators and scavengers of other meiofauna. There also are grazers that eat the diatoms and other tiny algae that live in the upper few millimeters of the sediment. The meiofauna, in turn, are part of the diet of many deposit feeders.

The underground world of the meiofauna is packed with bizarre creatures. There are protozoans, wiggling nematodes, tiny attached hydroids that capture their food with snake-like tentacles, and vacuum-cleaning worms. Some members are just miniature versions of flatworms, polychaetes, copepods, and other more familiar animals that live elsewhere. Some belong to groups found nowhere else. This is the case of **gnathostomulids** (phylum **Gnathostomulida;** see "How to Discover a New Phylum," p. 128) and **kinorhynchs** (phylum **Kinorhyncha**). Only 150 species of kinorhynchs are known, all restricted to marine mud and sand. Their bodies are divided into segments armed with spines. The head, which is also surrounded by spines, can be retracted into the body.

Gastrotrichs (phylum **Gastrotricha**) use suction to eat detritus and smaller members of the meiofauna. They have short, hair-like cilia on the head and the ventral surface of the body. About half the 450 known species are marine. Though they look much like protozoans, gastrotrichs have many cells and true tissues and organs.

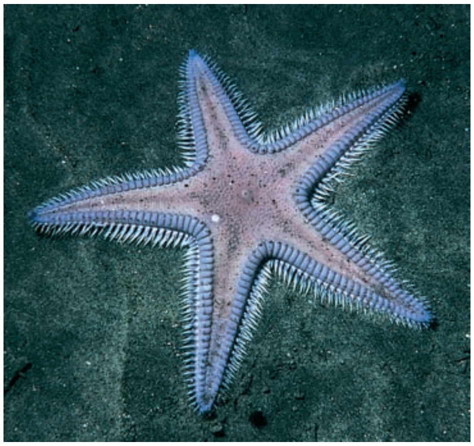
Rotifers (phylum **Rotifera**) are a group of nearly 2,000 known species, of which only about 100 are marine. Of these, several species are part of the meiofauna. They are known as "wheel animals" because of a crown of cilia on their heads. This structure is used in locomotion and feeding.

The **archiannelids** are segmented worms (phylum **Annelida**) that are very common members of the meiofauna. They are simple in structure and minute in size. Unlike polychaetes, the group of segmented worms in which they are often included, archiannelids typically lack distinct segments, parapodia, or bristles.

Oligochaetes are segmented worms that are widely distributed on land and in fresh water. They include the earthworms. Oligochaetes are less common at sea, but some are members of the meiofauna, especially in polluted bays and harbors.

Collecting and extracting live meiofauna is not particularly complicated. The easiest procedure is to take moist mud or sand and let it stagnate in a container for an hour or so. The meiofauna will move to the top layer of sediment as they run out of oxygen. Samples are taken close to the surface with an eyedropper and observed under a dissecting or, even better, a compound microscope. The show is about to begin.

FIGURE 13.14
Sea stars such as *Astropecten* prey on clams and other burrowing invertebrates.



The **Indo-West Pacific region** has the most species of seagrasses. Typical seagrass beds in this region consist of several species of seagrasses living together. Among the most common are turtle grass (*Thalassia*), paddle grass (*Halophila;* see Fig. 6.13*c*), strapweed (*Amphibolis*), and ribbonweed (*Posidonia*).

Pelagic Pertaining to the water column away from the bottom or other structure.

- Chapter 10, p. 220; Figure 10.11

Indo-West Pacific Region The tropical Indian and western and central Pacific oceans.

- Chapter 14, p. 315

EYE ON SCIENCE

Seagrass Wasting Disease

Seagrass beds have been adversely affected around the world by dredging, damage by boat propellers, and pollution, most especially by excess nutrients from agriculture and urban runoff. Disease has also had devastating effects. An epidemic of seagrass wasting disease resulted in about 95% loss of beds on the Atlantic coasts of North America and Europe in the 1930s. Some beds never recovered and disappeared forever. More recent but less dramatic outbreaks have taken place among seagrasses in the Atlantic and Pacific. Wasting disease, as well as other outbreaks of diseases among marine organisms, seems to be somehow related, directly or indirectly, to the impact of humans on the marine environment.

It was not until relatively recently that the cause of seagrass wasting disease was discovered. There is mounting evidence that the disease is caused by *Labyrinthula,* a microscopic, ameba-like organism with unclear affinities to the protozoans (see “Protozoans: The Animal-Like Protists, p. 97). *Labyrinthula* produces a network of filaments along which its cells move and absorb nutrients from seagrasses and seaweeds. Some species are even found in turf grasses on land! Species of *Labyrinthula* infect seagrasses such as eelgrass (*Zostera marina*) in temperate regions and turtle grass (*Thalassia testudinum*) in the tropics. *Labyrinthula* spreads through direct contact between attached plants and by drifting leaves. It produces enzymes that break down the contents of host cells, causing dark-brown to black spots and streaks on the leaves, eventually forming large patches. *Labyrinthula* is known to reduce the efficiency of photosynthesis by the host, ultimately killing the plant.

One puzzling aspect of *Labyrinthula* is that it has been found in plants that show no symptoms. It thus appears that some unknown environmental factor such as abnormally high salinities or temperatures, as well as perhaps the health of the plants, may trigger the appearance of symptoms. A complicating factor is that different species and strains of *Labyrinthula* may cause the disease, while others may not.

Research is now being undertaken at various institutions in the Gulf of Mexico coast of the United States and in Europe on the chemical defenses of seagrasses and their potential role on wasting disease. Seagrasses are known to produce substances that have antimicrobial properties and that may make plants resistant to *Labyrinthula* and outbreaks of the disease. These substances, called phenolic acids, have been found in healthy and diseased plants. Initial experiments with turtle grass, however, have shown that phenolic acids do not accumulate in response to the presence of *Labyrinthula*. Current research aims at determining the presence of other chemical responses that are induced by *Labyrinthula* and investigate their potential role in resistance by the plants. Also being investigated are the possible effects of changing environmental conditions on the production of phenolic acids and other antimicrobial substances and therefore on the susceptibility of plants to wasting disease. Different populations of seagrasses may show different susceptibilities to *Labyrinthula* as the result of genetic differences. It has been hypothesized that different genetic strains of *Labyrinthula* may live on different strains of seagrasses and that outbreaks occur when alien forms of *Labyrinthula* invade a new geographical region. What factors may influence such invasions? What types of human factors may be linked to invasion by *Labyrinthula* or to stress in seagrass plants that may facilitate outbreaks of wasting disease?

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

Turtle grass (see Fig. 6.13*d*) is the most common seagrass in the tropical and subtropical Atlantic. Extensive meadows are found to depths of about 10 m (33 ft), deeper in clear water. Manatee grass (*Syringodium;* see Fig. 6.13*a*) is often found together with turtle grass.

Eelgrass (*Zostera marina;* see Fig. 6.13*b*) is widely distributed in temperate and cold waters of the Pacific and North Atlantic. It is most common in shallow water, sometimes exposed at low tide (Fig. 13.15), but has been found at depths of up to 30 m (100 ft). *Posidonia oceanica*, another temperate species, is particularly important in the Mediterranean.

Seagrasses can grow into thick, luxuriant beds, which often consist of more than one species of seagrass and many species of seaweeds. Their roots and a network of underground stems (see Fig. 6.13) keep them anchored in the face of turbulence. The roots and stems also help stabilize the soft bottom, and the leaves cut down wave action and currents. This decrease in turbulence causes more and finer sediment to be deposited, which in turn affects colonization by other organisms. Turtle grass is particularly important in Caribbean coral reefs, where it helps stabilize the landward, shallow sides of the reefs. Reduced turbulence also improves water clarity because less sediment remains suspended in the water column.

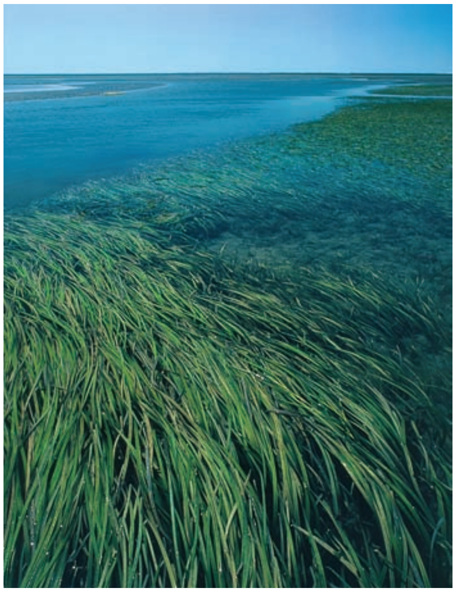


FIGURE 13.15 An extensive eelgrass (*Zostera marina*) bed on the Pacific coast of Baja California, Mexico.

Seagrass beds contain a very high plant **biomass,** as high as 1 kg/dry wt/m^2 for turtle grass. With such a high density of photosynthesizing plants, seagrass beds have a higher primary production than anywhere else on soft bottoms. In fact, they rank among the most productive communities in the entire ocean. Values as high as 8 gC/m^2/day (where gC is grams of carbon fixed) have been recorded for seagrasses alone. Part of the reason for such high primary production is

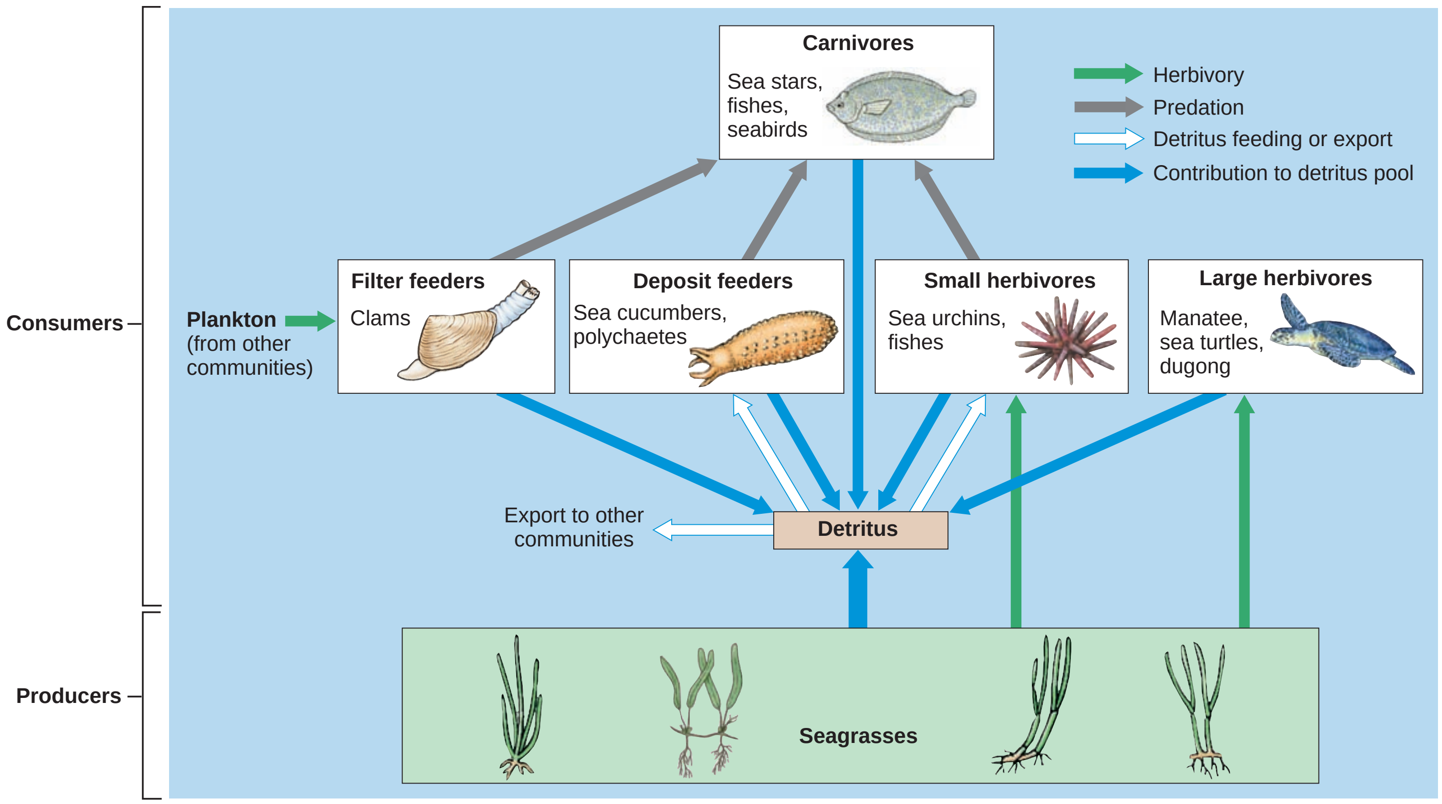

Carnivores
Sea stars, fishes, seabirds
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Consumers
Plankton (from other communities)
Filter feeders
Clams
Deposit feeders
Sea cucumbers, polychaetes
Small herbivores
Sea urchins, fishes
Large herbivores
Manatee, sea turtles, dugong
Export to other communities
Detritus
Producers
Seagrasses

FIGURE 13.16 Generalized food web in a seagrass community. As in estuaries (see Fig. 12.23), detritus generated from dead plants is an important source of food for many animals.

the fact that seagrasses have true roots, unlike seaweeds, and are therefore able to absorb nutrients from the sediment. Phytoplankton and seaweeds, by contrast, must depend on nutrients dissolved in the water column. Some typical rates of primary production in seagrass beds and other marine environments are summarized in Table 10.1 (p. 225).

Many small algae grow on the surface of seagrass leaves. These algae, known as **epiphytes,** further increase primary production in seagrass communities. Microscopic diatoms are particularly abundant. Some epiphytic cyanobacteria also carry out **nitrogen fixation** and release nutrients in the form of nitrogen compounds.

The number of grazers, or herbivores, varies with geographical location. Herbivores, not many of which eat seagrass leaves, directly consume much less than half of seagrass primary production. Herbivores that do eat seagrasses include sea turtles, manatees, sea urchins, and some parrotfishes. Seagrasses are also important in the diet of some birds, such as ducks and geese in the Arctic and other regions.

Animals take advantage of the high primary production of seagrasses in several ways, even when they do not actually eat the seagrasses themselves (Fig. 13.16). Many feed on the large amounts of decaying leaves and seaweeds. Deposit-feeding polychaetes, clams, and sea cucumbers live in or on the detritus-rich sediment. Detritus is also exported to other communities, such as the unvegetated soft bottoms of deeper water.

The dense seagrasses also offer shelter to many animals that do not feed on detritus. More animals live in or on the sediments in seagrass beds than in the surrounding unvegetated sediments. A variety of small sessile or crawling animals live on the leaves: hydroids, snails, tiny tube-dwelling polychaetes, amphipods, shrimps, and the like (Fig. 13.17). Larger animals such as the queen conch (*Strombus gigas,* Fig. 13.18), live among the plants. Filter feeders that live in the sediment include clams and the pen shell (*Pinna carnea*). Several species of fishes and the West Indian sea star (*Oreaster reticulatus*) are examples of carnivores. Seagrass beds also serve as nurseries for commercially valuable species such as the Atlantic bay scallop (*Argopecten irradians*) and shrimps.

Highly productive seagrass communities are restricted to soft bottoms in shallow, sheltered water. The plants are not heavily grazed but produce a lot of detritus that is used by deposit feeders and exported to other communities.

Hard-Bottom Subtidal Communities

Hard bottoms make up a relatively small portion of the continental shelf. Usually, they are just the submerged extensions of rocky shores. There are also some subtidal rocky outcrops of varying

Biomass The total weight of living organisms.
- Chapter 10, p. 223

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.
- Chapter 5, p. 93; Table 5.1.

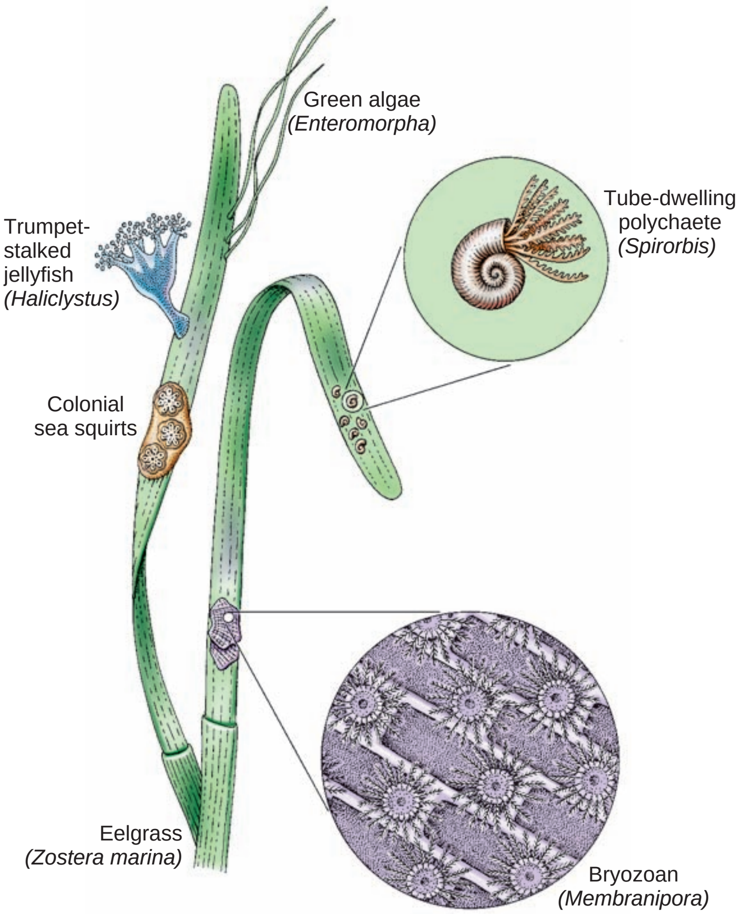


FIGURE 13.17 Eelgrass (*Zostera marina*) leaves are often inhabited by sessile, or attached, organisms.

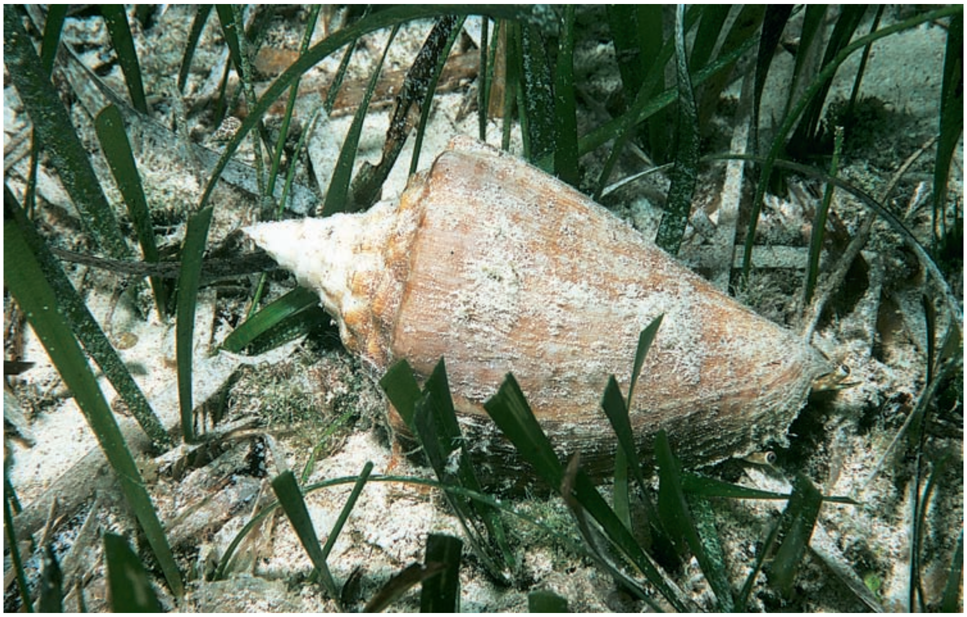


FIGURE 13.18 The queen conch (*Strombus gigas*) is a large snail commonly associated with turtle grass beds in Florida and the Caribbean. It is highly prized as food.

size. In some cases a significant component of the hard substrate is provided by **calcareous algae,** the tubes of polychaete worms, and oyster shells (see Fig. 12.22). These three-dimensionally complex hard bottoms are often called reefs, but they should not be confused with the coral reefs of warm waters.

Rocky Bottoms Unlike those in the intertidal, the communities that develop on subtidal rocky bottoms are never subject to desiccation. This means that a wider variety of organisms can live there than in the intertidal.

Rocky-bottom communities in shallow water are rich and productive. Seaweeds are the most conspicuous inhabitants, especially on flat or gently sloping bottoms. They occur in an awesome array of colors, growth forms, textures, and sizes. Most are brown and red seaweeds. They can be filamentous (*Chordaria, Ceramium*), branched (*Agardhiella, Desmarestia*), thin and leafy (*Porphyra, Gigartina*), or **encrusting** (*Lithothamnion*). Many of these species can also be found in the intertidal.

As in the intertidal, one of the main problems for seaweeds and sessile animals in the subtidal is to find a place to attach. Practically all seaweeds have a **holdfast** (see Fig. 13.21) to anchor them to the substrate. Every bit of space is occupied, even if it seems clean to our naked eye. Thus, there is intense competition for living space on the rocks. Different species of seaweed have different competitive abilities. They also vary in their tolerance to wave action, grazing by sea urchins and other herbivores, temperature, light, and the stability of the substrate.

The effect of light is particularly intriguing. As depth increases, the amount of light available for photosynthesis decreases, making it harder for seaweeds to live there. Some species are better adapted to deep water than others, however. Several can live at depths of over 200 m (650 ft) in clear water. Deep-water seaweeds have increased levels of chlorophyll and other pigments that capture light energy. These adaptations can be found in all groups of seaweeds and are not restricted to the red algae, once thought to be the best adapted to deep water. In any case, depth zonation is not determined by light alone. It is affected by grazing, competition for space, and other factors.

Seaweeds also vary in their life history strategies. Some are **perennial** and are found year-round, whereas others are found only at certain times. Though some grow fast and are short-lived, others grow slowly and are sturdy and long-lived. Fast growers are typically the first to colonize surfaces recently disturbed by grazers, turbulence, or other phenomena. Some seaweeds use both strategies by alternating a fast-growing, short-lived stage with a slow-growing, perennial one. Many have different growth forms at different times of their lives (see Fig. 6.11). Growth forms belong to the same species but look and function differently.

Seaweeds must compete for space not only with each other but also with many sessile animals. Invertebrates tend to dominate on steeply sloping bottoms and vertical walls, where light limits seaweed growth. Hard substrates provide a good place for organisms to attach but are much harder to burrow through than sand or mud. As a result, hard-bottom communities tend to have a rich epifauna and a poor infauna, the reverse of soft-bottom communities. Sponges, hydroids, sea anemones, soft corals, bryozoans, tube-dwelling polychaetes, barnacles, and sea squirts are among the most common groups. Many form colonies that outcompete other species by simply growing over them. A few, such as the rock-boring clam (*Pholas*), live embedded in rocks.

Grazers on subtidal rocky bottoms are usually small, slow-moving invertebrates. Perhaps most important are sea urchins (*Arbacia, Diadema, Strongylocentrotus;* Fig. 13.19). Chitons, sea hares, limpets, abalones (*Haliotis*), and other gastropod mollusks, as well as several groups of fishes, are also important grazers (Fig. 13.20).

Some seaweeds have evolved defenses against grazing. These include chemicals, such as sulfuric acid and phenols, that make them unpalatable and the ability to rapidly regrow tissue lost to grazers. Some seaweeds even have life history stages that bore into mollusc shells, a good deterrent to being eaten by a hungry sea urchin! Upright seaweeds tend to be tough and leathery. Calcareous algae, which include coralline (*Lithothamnion, Clathromorphum*) and calcareous green (*Halimeda;* see Fig. 14.10) algae, deposit calcium carbonate in their cell walls, making them particularly resistant to grazing.

Carnivores, including nudibranchs and other gastropods and sea stars, feed on attached invertebrates. Sea urchins feed not only on seaweeds but also on some of the flimsier attached invertebrates. Other carnivores, such as crabs, lobsters, and many types of fishes, prey on grazers and smaller carnivores.

Grazers and predators strongly influence the composition of hard-bottom

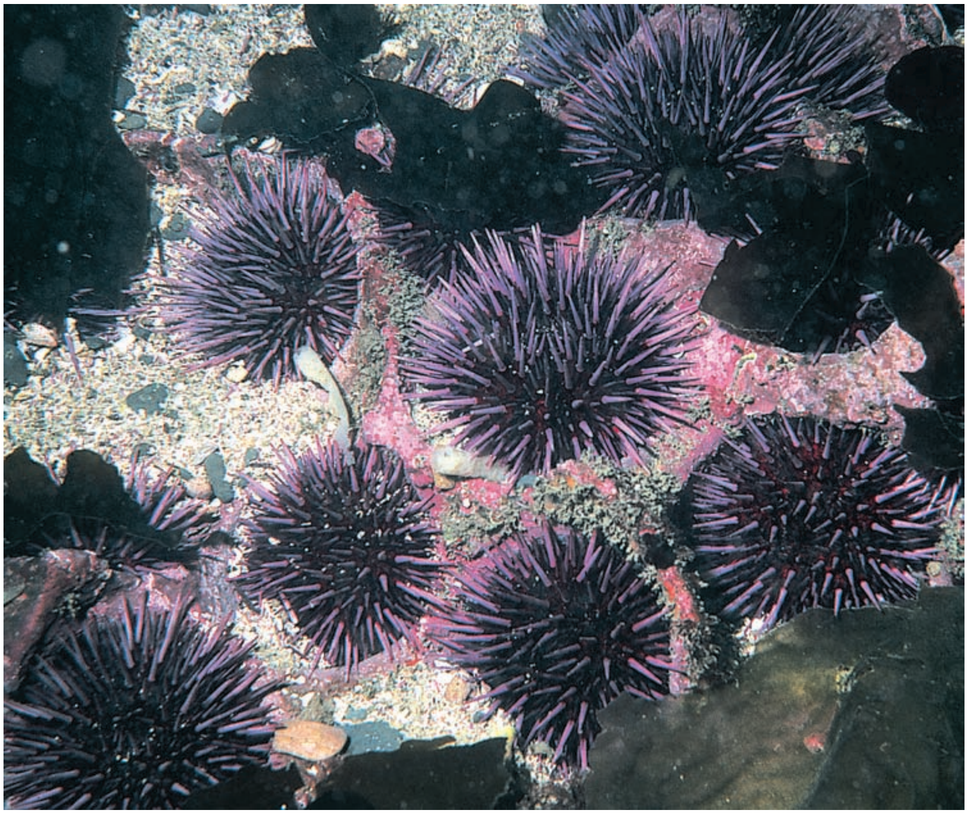


FIGURE 13.19 Sea urchins, like *Strongylocentrotus purpuratus* from the Pacific coast of North America, are important in influencing the composition of hard-bottom subtidal communities. They graze on seaweeds and on some of the encrusting animals and thus uncover new surfaces where other sessile organisms can settle.

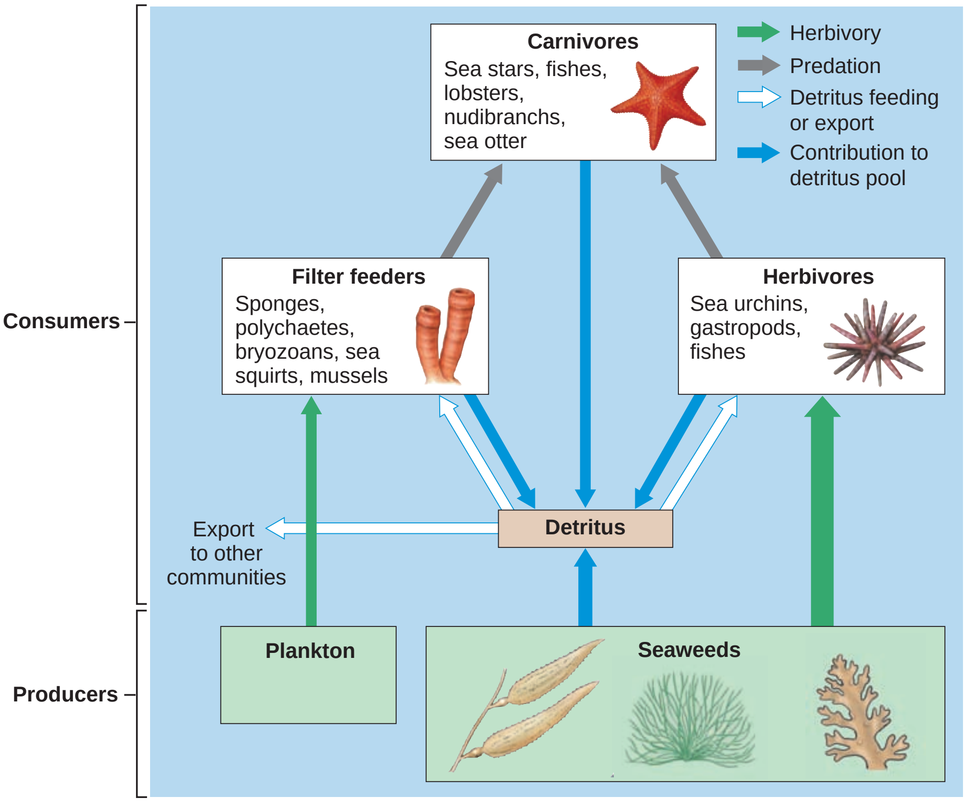

Carnivores
Sea stars, fishes, lobsters, nudibranchs, sea otter
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Filter feeders
Sponges, polychaetes, bryozoans, sea squirts, mussels
Herbivores
Sea urchins, gastropods, fishes
Consumers
Export to other communities
Detritus
Plankton
Seaweeds
Producers

FIGURE 13.20 Generalized food web in a hard-bottom subtidal community. Most of the detritus generated is in the form of drift seaweeds.

Encrusting Seaweeds Those that grow as a thin layer over rocks, such as some of the coralline algae.

- Chapter 6, p. 107

Sunlight penetrates through the water column to depths that depend on water transparency. Not all colors of light penetrate to equal depths. In clear ocean water, blue light penetrates the deepest, red the least.

- Chapter 3, p. 47; Figure 3.11

communities. As in the rocky intertidal (see Fig. 11.22), they remove residents from the rocks, opening up space for other organisms. Settling larvae and seaweed spores colonize the patches cleared by grazers and carnivores. Because these planktonic stages are often seasonal, patches formed at different times may be colonized by different species. This increases species diversity in a given area. Carnivores may also act as a check on the grazers, helping maintain a relatively stable situation. This balance can be easily upset, however. For example, explosive increases in sea urchin populations have been reported in several subtidal communities (see p. 300), as have mass mortalities. Like all biological communities, subtidal communities are constantly changing.

The species composition of rocky-bottom subtidal communities is influenced by factors such as light, competition for space, grazing, and predation.

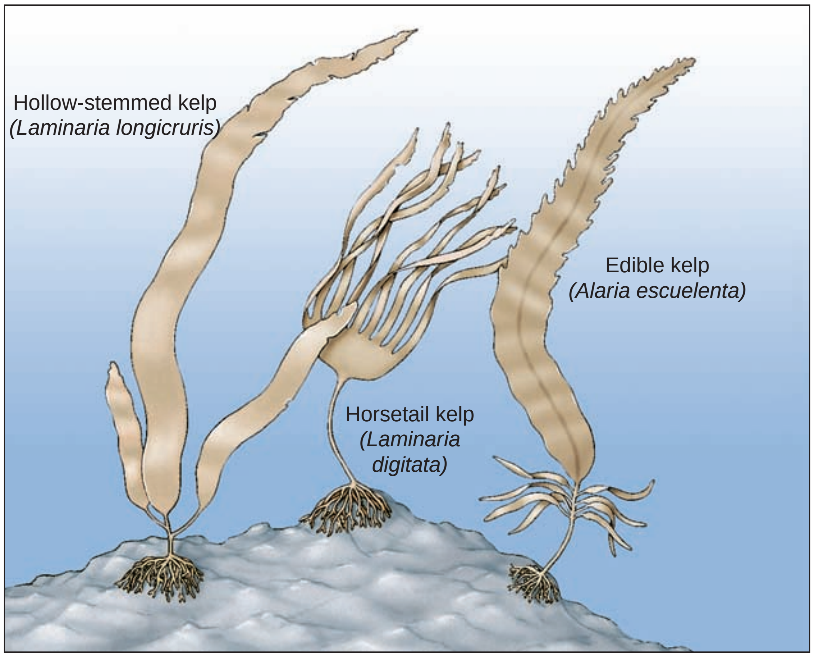


FIGURE 13.21 Examples of North Atlantic kelps. The hollow-stemmed kelp reaches lengths of 12 m (40 ft) in deeper water.

Kelp Communities Among the most fascinating of marine communities, **kelp communities** are also one of the most productive. Kelps are a group of large, fast-growing brown seaweeds that live in relatively cold water and are restricted to temperate and subpolar regions. (see "Brown Algae," p. 104). They are true giants compared with other subtidal seaweeds or seagrasses, creating luxuriant forests (see Fig. 6.8) that are home to a vast assortment of organisms.

There are several species of kelp. In the North Atlantic and on the Asiatic coast of the North Pacific, various species of *Laminaria* (Fig. 13.21) predominate. Their simple or cleft blades may be 3 m (10 ft) long. The giant kelp (*Macrocystis*) dominates kelp communities on the Pacific coasts of North and South America and other parts of the Southern Hemisphere (Fig. 13.22). Each kelp individual is attached to the rocky bottom by a large holdfast (see Fig. 6.1). Several long **stipes,** intertwined to form a trunk-like foundation, grow from a single holdfast. The **fronds,** leaf-like blades, grow from the stipes. A single stipe can reach 20 to 30 m (65 to 100 ft) or more. In some Southern Hemisphere communities, *Ecklonia* rather than *Macrocystis* is the main species (see photo on p. 283). Kelp communities on the Pacific coast of North America are particularly diverse. A number of species, including the bull kelp (*Nereocystis*), the elk kelp (*Pelagophycus;* Fig. 13.23), *Alaria,* and *Pterygophora,* may be important or even replace *Macrocystis.* The bull kelp consists of many blades, each up to 5 m (16 ft) long, that hang below the surface suspended by a gas-filled **pneumatocyst** located at the end of a long stipe. *Alaria* (Fig. 13.21), which like many other species of kelp is edible, is also important in the North Atlantic.

Large, dense patches of kelp are known as **kelp beds.** They are called **kelp forests** when the fronds float on the surface in a thick mat (Fig. 13.24). This floating **canopy** is characteristic of Pacific kelp forests dominated by the giant and bull kelps. *Ecklonia* and some species of *Laminaria* and *Alaria* also form a canopy.

Physical factors have a major influence on kelp communities. Temperature is of particular importance because kelps are restricted to cold water. This is partially because kelps don't do well in warm water and partially because warm waters tend to lack the rich supply of nutrients that kelps need (see "Patterns of Production," p. 346). This dependence on cold water is reflected in the geographic distribution of kelps (Fig. 13.22). The surface waters of the oceans flow in great clockwise gyres in the Northern Hemisphere and counterclockwise gyres in the Southern Hemisphere (see Fig. 3.21). The currents that flow toward the poles on the western sides of the oceans carry warm water from equatorial regions. Because of this, kelps are restricted to high latitudes on the western sides of the oceans. On the other hand, kelps extend well down eastern shores, where cold, nutrient-rich currents flow down from high latitudes. *Ecklonia* occurs in low latitudes not far from the Equator along the southern coast of the Arabian Peninsula (Fig. 13.22). It is found there only during the summer, when the summer **monsoons** that blow northeastward across the Arabian Sea cause strong **upwelling** that lowers water temperature (see Fig. 15.31). The disappearance of the monsoons when the winds reverse direction during the winter causes an increase in water temperature, which kills the kelp.

All but a few species of kelp are limited to hard surfaces, which may include substrates such as worm tubes and the holdfasts of other seaweeds. Given a suitable place to attach, kelps will grow in water as deep as light allows. This can be quite deep, up to 40 m (130 ft) in some species. Their fronds float at the surface, basking in sunlight, while their stipes connect them to the bottom far below.

Kelps are actually quite fragile for their giant size; in fact, they are fragile largely *because* of their size. The fronds cause a lot of drag, but the long, thin stipe breaks easily, and kelps are often torn from the bottom. Drifting kelps cause more damage by entangling other fronds. Kelps don't do well where there is heavy wave action, and

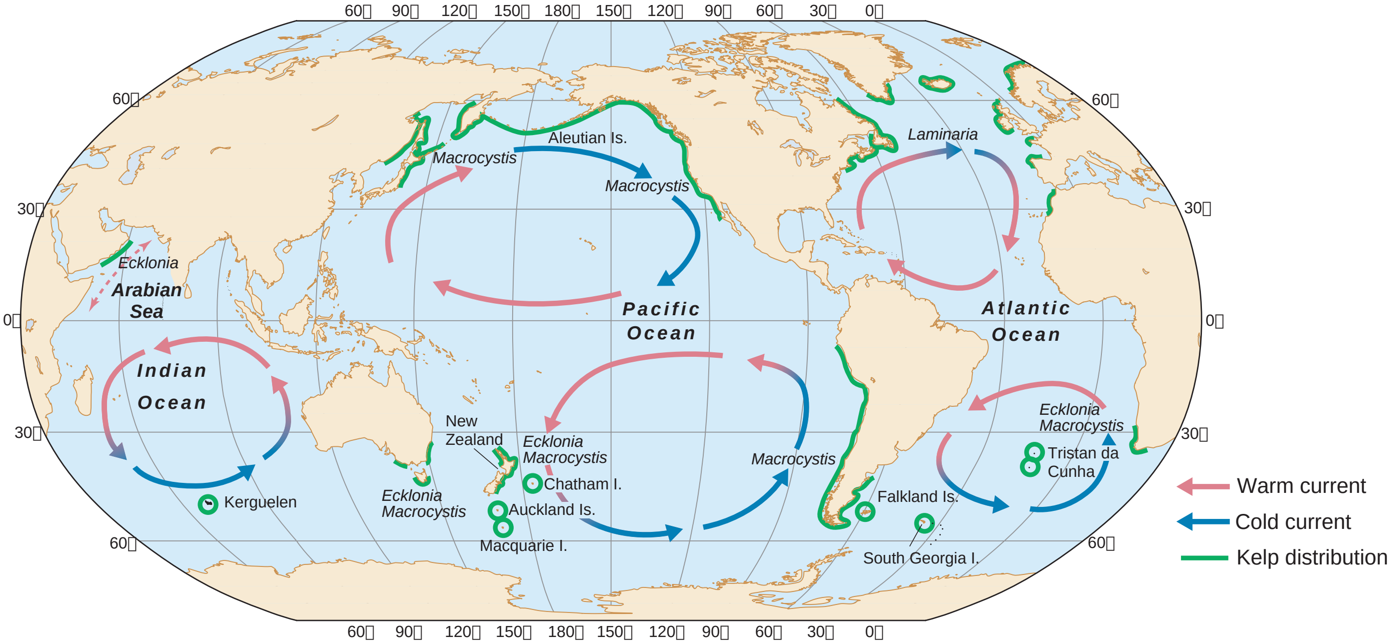

60°
90°
120°
150°
180°
150°
120°
90°
60°
30°
0°
60°
30°
0°
30°
60°
Macrocystis
Aleutian Is.
Macrocystis
Laminaria
Ecklonia
Arabian Sea
Pacific Ocean
Atlantic Ocean
Indian Ocean
New Zealand
Ecklonia
Macrocystis
Chatham I.
Macrocystis
Ecklonia
Macrocystis
Tristan da Cunha
Kerguelen
Ecklonia
Macrocystis
Auckland Is.
Macquarie I.
Falkland Is.
South Georgia I.
Warm current
Cold current
Kelp distribution

FIGURE 13.22 The geographic distribution of kelps is greatly affected by surface temperatures, which are influenced by the surface circulation of the ocean. Currents along the west sides of the continents transport cold water from polar regions; on the east sides warm water is transported away from the Equator. As a result, kelps extend farther toward the Equator along the west sides of the continents than on the east sides. The opposite is true for reef-building corals, which require warm water (also see Fig. 14.11).

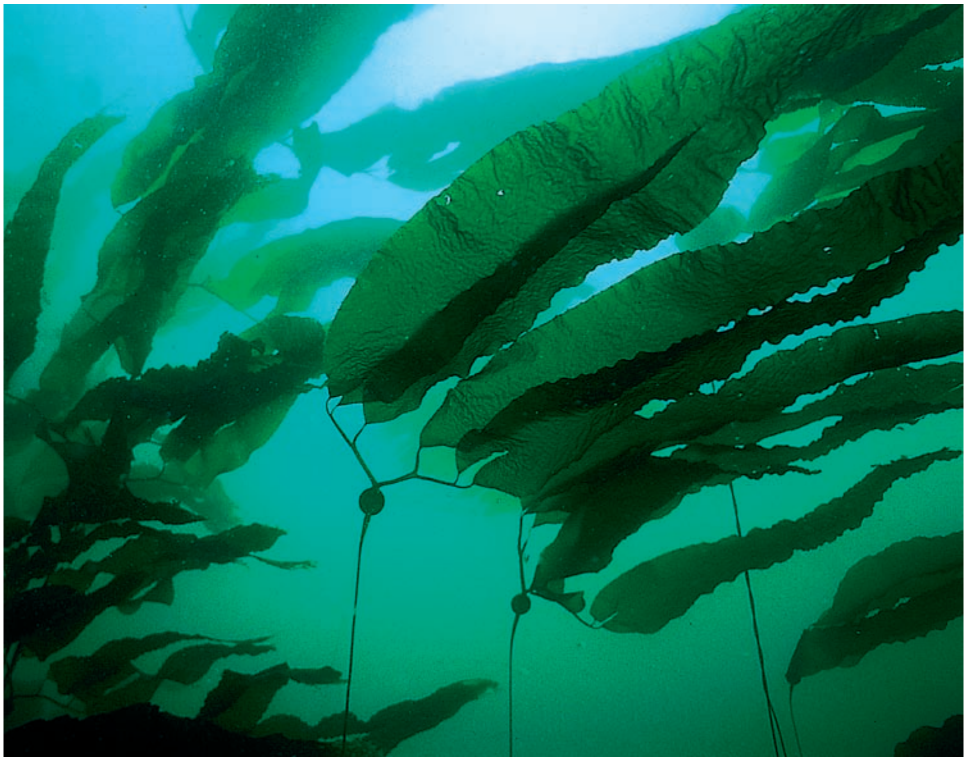


FIGURE 13.23 The elk kelp (*Pelagophycus porra*) grows on the outer, deeper edges of some giant kelp beds (see Fig. 13.26). It has two impressive, antler-like branches from which large blades hang at the mercy of the currents.

storms can be disastrous. Though they must extend their blades to the surface, many species prefer to attach to the bottom in relatively deep water, where wave action is reduced. Thus, the very adaptations that allow these species of kelp to live in deep water, large size and floating fronds, also tend to restrict them there.

Kelps can grow very fast, with the giant kelp growing as fast as 50 cm/day (20 in/day). Not surprisingly, kelp communities are very productive. Primary production reaches 1,000 gC/m^2/year in *Ecklonia* in Australia and South Africa, around 1,500 gC/m^2/year in California giant kelp, and close to 2,000 gC/m^2/year in *Laminaria* in the North Atlantic (also see Table 10.1, p. 225).

Kelp communities are restricted to hard substrates in cold, nutrient-rich water.

The large kelps we see are only one stage in their life history. All kelps go through two stages: a large, spore-producing **sporophyte** and a microscopic **gametophyte,** which produces male and female gametes (Fig. 13.25). The sporophyte is the organism we see.

Monsoons Winds in the northern Indian Ocean that blow from the southwest in summer but from the northeast in the winter.

- Chapter 15, p. 352; Figure 15.31

Upwelling The upward flow of cold, nutrient-rich deep water to the surface.

- Chapter 15, p. 351

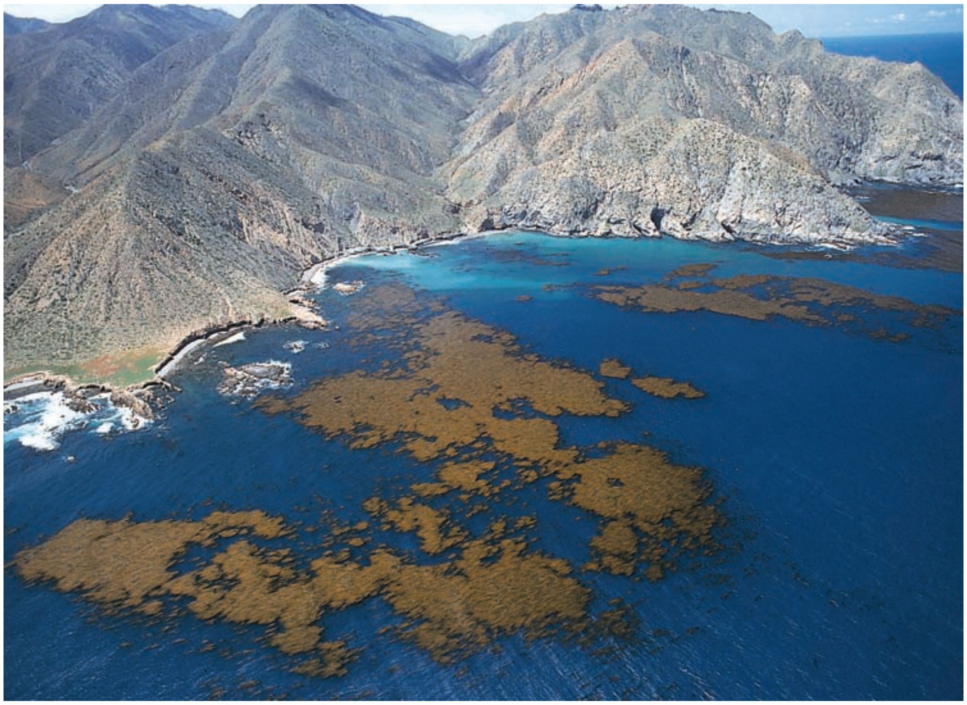


FIGURE 13.24 Giant kelp (*Macrocystis pyrifera*) forest at Cedros Island, Baja California, Mexico.

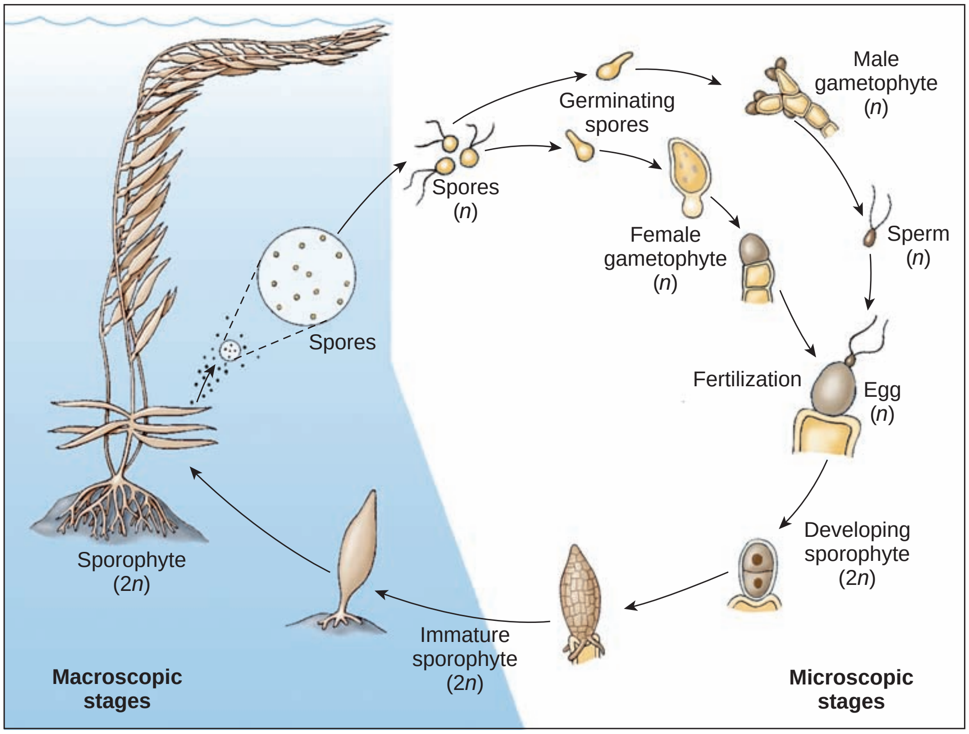


FIGURE 13.25 The life history of the giant kelp (*Macrocystis*) and other kelps includes a large, spore-producing sporophyte. Spores settle on the bottom and develop into minute male or female gametophytes. Each gametophyte releases male or female gametes, which, after fertilization, develop into the sporophyte, thus completing the cycle (also see Fig. 6.11*a*).

In some kelps the sporophyte is an annual. In contrast, the giant kelp and others are perennial and can live for several years. These long-lived kelps often lose fronds to grazers, storms, and waves. They are able to grow them back because, unlike many seaweeds, growth takes place at the holdfast as well as the end of the stipes.

Kelp forests along the Pacific coast of North America are arranged in distinct depth zones, each made up of species that grow at a characteristic height above the bottom (Fig. 13.26). This structure results from the interaction of several physical and biological factors. The floating canopy of the giant kelp, for instance, develops only where the water is deep enough to reduce wave action but shallow enough for light to reach the bottom, permitting growth from the holdfasts. Other kelps may contribute to the surface canopy. These include the bull kelp, found closer inshore, and the feather-boa kelp (*Egregia*), which lives in shallower water subject to wave action. The elk kelp forms a midwater canopy in deeper water along the outer edge of the giant kelp canopy.

The dense canopy of giant kelp forests cuts down the amount of light underneath. Diving under the canopy is like walking into a dense forest on land: It takes a few moments for your eyes to adjust to the dim light. The kelps that live there also have to adapt to the reduced light level, but life under the canopy is rich and varied. Smaller kelps exploit the **understory,** the area below the canopy. They include *Laminaria, Pterygophora,* and other kelps that have either erect fronds that stand above the bottom or fronds that lie right on it.

A variety of shorter algae, mostly red algae, live on the bottom under the two overlying layers, even when light is greatly reduced. Both branching and encrusting coralline algae are common. Some seaweeds are more abundant in shallow water, where increased wave action reduces the canopy.

North Atlantic kelp beds are dominated by species of *Laminaria* that typically do not form a canopy. They are similar to Pacific kelp forests, however, in that they include many species of seaweeds and are arranged in depth zones.

The complex, three-dimensional structure of kelp communities is exploited by many different animals. An assortment of polychaetes, small crustaceans, brittle stars, and other small invertebrates live on the kelp holdfasts, particularly those of the giant kelp. Tube-dwelling polychaetes and other sessile organisms are common on the blades and stipes. Like the animals that live associated with the holdfast, they are mostly suspension feeders. One conspicuous inhabitant of the blades is a bryozoan

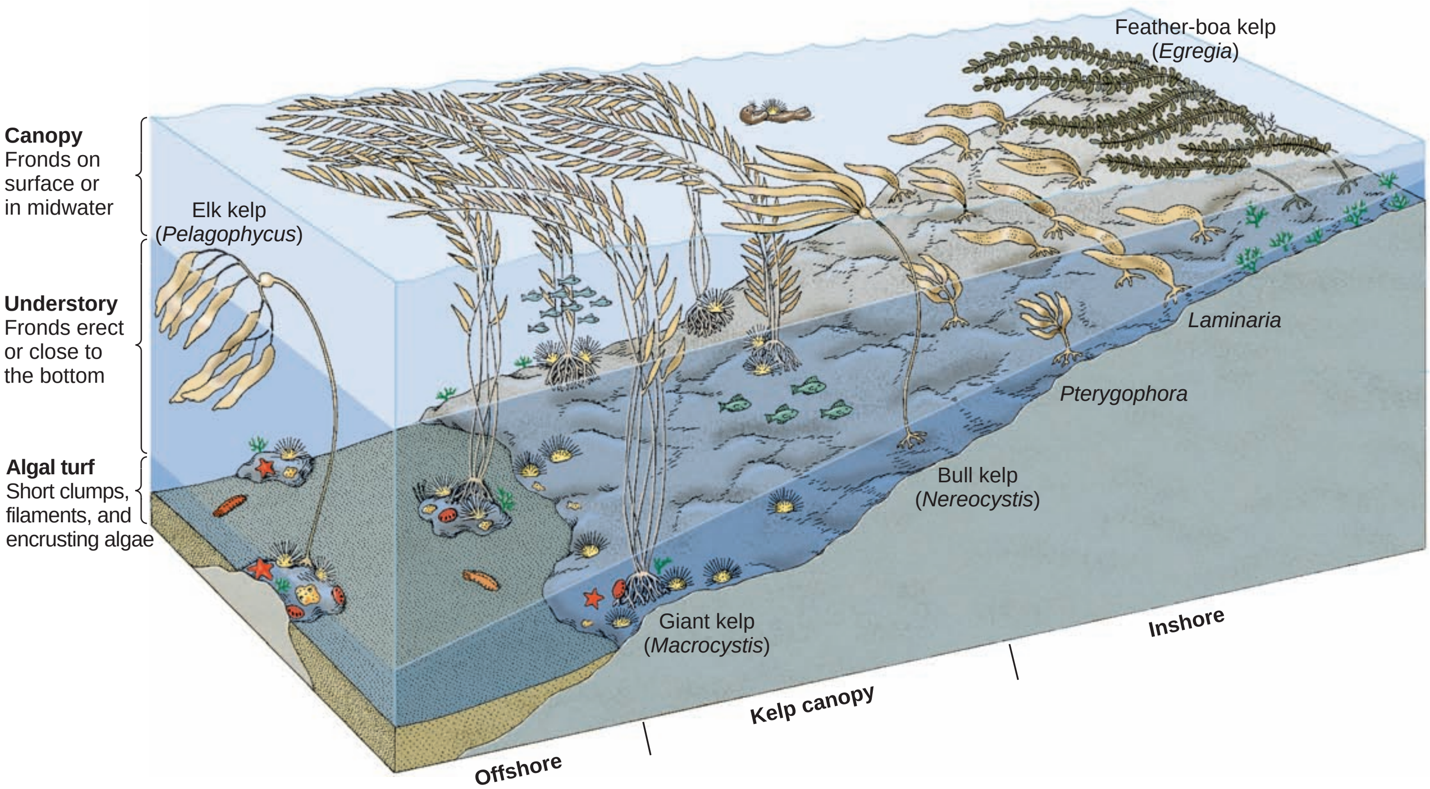

Canopy
Fronds on surface or in midwater
Understory
Fronds erect or close to the bottom
Algal turf
Short clumps, filaments, and encrusting algae
Elk kelp (*Pelagophycus*)
Feather-boa kelp (*Egregia*)
Laminaria
Pterygophora
Bull kelp (*Nereocystis*)
Giant kelp (*Macrocystis*)
Inshore
Kelp canopy
Offshore

FIGURE 13.26 Distribution of the major types of kelps and other seaweeds in a generalized giant kelp (*Macrocystis*) forest on the Pacific coast of North America. The complex distribution of algae results from the effects of factors such as light, type of substrate, wave action, depth, number and type of grazers, and even time of year because some of the seaweeds are annuals.

(*Membranipora*) that forms thin, lace-like colonies. Its calcareous encrustations weigh the blades down and cover photosynthetic tissues, but their effect appears to be minimal. The rocky bottoms around kelps are inhabited by sponges, sea squirts, lobsters, crabs, hermit crabs, sea stars (see Fig. 7.45*a*), abalones (see Fig. 7.22*b*), and octopuses, among others.

Fishes are very common in kelp communities. They use the food resources and shelter provided by the kelp community in many ways, thus occupying many different **ecological niches.** For instance, fishes often use the available resources by feeding and taking shelter in different areas within the forest. Some species feed close to the bottom. In kelp beds along the Pacific coast of North America, bottom feeders include many species of rockfishes (*Sebastes*) and the kelp bass (*Paralabrax clathratus*). The California sheephead (*Semicossyphus pulcher*) uses its dog-like teeth to crush sea urchins, crabs, and other bottom invertebrates. Surf-perches (*Rhacochilus, Brachyistius*) and others may feed in different parts of the canopy, around the holdfasts, or in the open water among the kelp. Topsmelt (*Atherinops*) are plankton feeders that take advantage of large swarms of opossum shrimps, or mysids, and other planktonic animals found around kelps. Fishes may define additional ecological niches by being active at different times of the day or night.

Small algae are grazed by snails, crabs, sea urchins, and fishes, but surprisingly few grazers eat the large kelps. One giant kelp grazer, the Steller's sea cow, is now extinct (see Fig. 18.13). Isopods (*Phycolimnoria*) are small crustaceans that burrow into the holdfast, weakening it. A few fishes graze on kelps, but they do not appear to cause much mortality. Instead of feeding on the attached, actively growing individuals, animals use most of the huge production of kelps in the form of drift kelp, pieces that break loose and sink to the bottom or are washed ashore. As with seagrasses, salt-marsh plants, and mangroves, much of this detritus is exported to other communities.

Kelp beds form a multistoried, complex environment. Drift kelp and understory seaweeds are a major food source but not the live kelp themselves.

Sea urchins are by far the most important grazers in kelp communities. Of special importance are the red (*Strongylocentrotus franciscanus*) and purple (*S. purpuratus*) sea urchins on the Pacific coast of North America and the green sea urchin (*S. droebachiensis;* see Fig. 7.47*a*) in both the North Atlantic and North Pacific. Sea urchin populations sometimes "explode" (see Fig. 10.3). These explosions have had devastating impacts on kelp communities in

Ecological Niche The combination of what a species eats, where it lives, how it behaves, and all the other aspects of its lifestyle.
- Chapter 10, p. 215

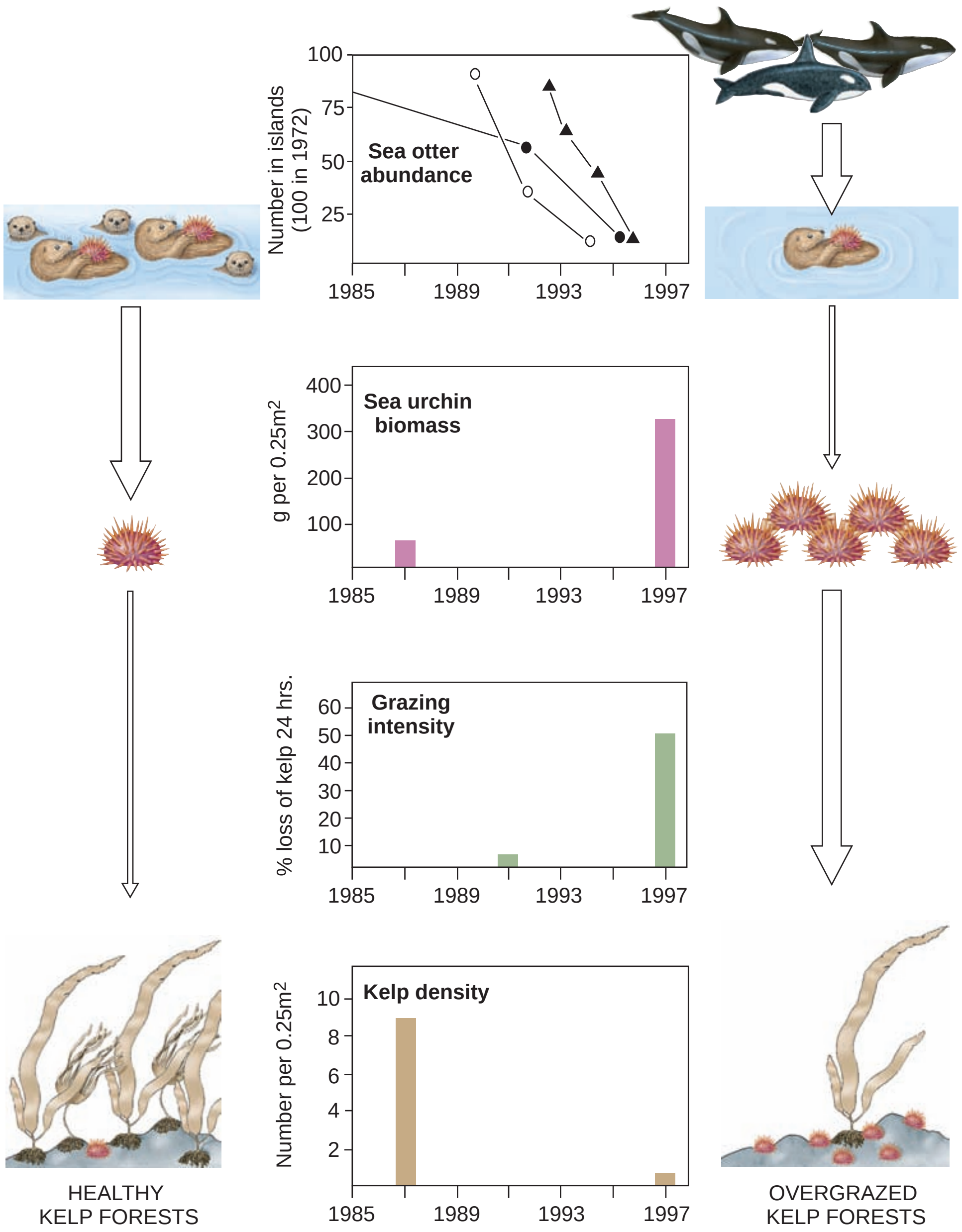


FIGURE 13.27 The effect of predation of sea otters (*Enhydra lutris*) by killer whales (*Orcinus orca*) on the populations of sea urchins and kelps in kelp forests in the Aleutian Islands, Alaska. The effect is an example of a trophic cascade, so called because the effects of a predator extend throughout the food web. In the graphs, years without bars indicate years without data and not zero values.

different parts of the world. Sea urchins normally feed on drift kelp. During population explosions, or "plagues," however, the urchins eat live kelps and other seaweeds. When the sea urchins eat the holdfasts or stipes, the kelps break loose, float away, and die. The sea urchins may even climb up the kelp, weighing down the fronds and allowing other urchins to reach them. The urchins may completely clear large areas, which are then known as "urchin barrens" or "urchin deserts." Encrusting coralline algae are virtually the only seaweeds left on these barrens.

The reasons for such outbreaks of urchins remain unclear. In the North Pacific a possible cause is the decline in sea otters (*Enhydra lutris;* see Fig. 9.12), an urchin predator that has disappeared from most of its former range. In a study of several islands in the Aleutian chain, Alaska, kelp forests were found to be healthy where sea otters were common. In contrast, there were many sea urchins and few kelps on islands where sea otters were absent (Fig. 13.27). There is evidence that otter populations have declined because of predation by killer whales, which normally prefer seals and sea lions. Seals and sea lions have become increasingly scarce since the late 1980s, perhaps because overfishing has reduced their food supply. Killer whales also appear to have changed their feeding habits when an important food source, the carasses of harpooned whales tied to whaling ships, dwindled when most commercial whaling was banned. Overfishing thus may have affected kelp forests by way of a chain of events that includes seals and sea lions, killer whales, sea otters, and sea urchins.

Observations in the Aleutians, however, do not help explain the situation in Southern California, where sea otters were wiped out almost 200 years ago, but the destruction of kelps by sea urchins was not observed until the 1950s. Heavy fishing on other urchin predators, including lobsters, crabs, and fishes, probably plays a role in the increase in urchin populations in Southern California and other places.

Another possibility is that a decrease in the amount of drift algae in Southern California might have caused the urchins to switch to feeding on live kelps. Sewage pollution and temperature increases are factors that may have caused a drop in the availability of drift kelp. Some of these factors may also stimulate the growth and survival of sea urchins. Some organic compounds released in sewage, for example, are used as nutrients by juvenile sea urchins.

The harvesting of Pacific abalones for food in Southern California has also been proposed as a possible cause of sea urchin plagues. These large molluscs compete with sea urchins for shelter in rock crevices. Removal of the abalones may provide more space for urchins.

It is also possible that fluctuations in the number of sea urchins are caused by the higher survival of their planktonic larvae, perhaps the result of more favorable temperatures or more abundant food. It is likely that a combination of factors causes urchin plagues, which probably are natural fluctuations in population size.

In addition to grazing by sea urchins, another factor affecting the health of kelp forests is climate. A strong **El Niño** in 1983 produced severe storms and unusually warm currents, which caused high kelp mortality. The 1997–1998 El Niño was similarly destructive. A **La Niña** that followed the 1997–1998 El Niño, however, brought cold, nutrient-rich currents to the California coast, stimulating the recovery of kelp forests.

Kelp communities may be severely disrupted by strong wave action, grazing by sea urchins, warm currents, and pollution.

The recovery of Southern California kelp forests has progressed well in a few areas. It has been aided in part by transplanting healthy kelps tied to blocks into depleted areas (see "Restoration of Habitats," p. 417). To appease fishers, who were angry at the possibility of sea otters feeding on valuable shellfish, it was agreed that sea otters were to be kept from naturally migrating from central to Southern California. A 2007 survey showed 3,026 sea otters along the California coast, a slight increase since a 2004 peak of 2,825 and continuing a recovery after decreases in numbers from 1995 to 2002. Sea otters are unfortunately being infected by protozoan parasites of humans. One such parasite is *Giardia,* which is found in the small intestines of humans, dogs, and cats. It has also been found in whales. *Toxoplasma,* a parasite carried by cats, has been linked to lethal brain infections in sea otters, seals, and dolphins. Marine animals get these parasites from sewage and urban-runoff pollution.

Will measures to stimulate the recovery of kelp beds have an effect on kelp beds? Nobody really knows. One thing is for sure: Some Southern California kelp forests have not recovered and perhaps never will.

A similar situation with a different cast of characters has been described in the Gulf of Maine on the Atlantic coast of the United States. Overfishing of cod (*Gadus*) and other bottom-feeding fishes reduced pressure on young lobsters (*Homarus*), crabs, and sea urchins. The number of sea urchins steadily increased and they grazed on kelp, which is used by lobsters as shelter. Heavy harvesting of sea urchins for export to Japan led to a reduction in their numbers in the early 1990s. This development and continued overfishing of bottom fishes have resulted in a sharp increase in the number of lobsters. A total of 28.5 million kg (63 million lb) of lobsters worth around $290 million were caught during the 2005 season, more than 2.5 times the 1945–1985 average.

Evidence from other parts of the world, however, seems to indicate that catastrophic disturbances of kelp communities are usually followed by a recovery, all in recurring cycles. Sea urchins and kelps are apparently kept in a delicate balance that can be tipped one way or the other by factors such as climate fluctuation, the effects of nutrient pollution on the survival of urchin larvae, and the removal of urchin predators.

El Niño A warming of the surface water in the Eastern Pacific, part of large-scale changes in atmospheric and ocean current patterns, or *ENSO*.
- Chapter 15, p. 353

La Niña A cooling trend of the surface water in the Eastern Pacific.
- Chapter 15, p. 355

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Eelgrass communities in Europe and the eastern coast of North America were severely affected by wasting disease in the 1930s, which caused many eelgrass beds to disappear. What changes would you expect to take place if an eelgrass community vanished from a given area? Consider changes to the substrate, the benthos, and other types of marine animals. Are there any possible changes among animals living on land? What type of community do you think would replace the eelgrass communities after they disappeared?
2. The life history of kelps consists of a very large sporophyte and a tiny gametophyte. Sea lettuce and some other seaweeds, however, have a gametophyte that is as big as their sporophyte (see Fig. 6.11*a*). Do you see any advantages for kelps having such an inconspicuous, puny gametophyte?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

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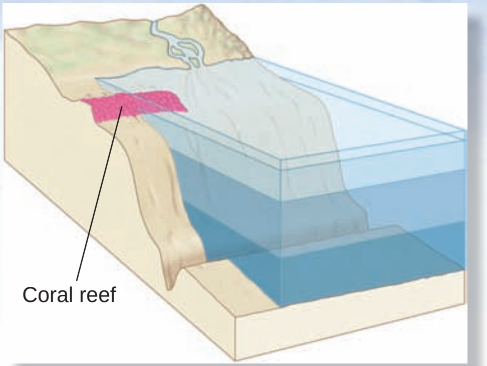
Reef flat on Majuro Atoll, Marshall Islands, in the western tropical Pacific.

14

CHAPTER

Coral Reefs



There is something special about tropical coral reefs. The warm, clear water, spectacular colors, and multitude of living things captivate almost everyone who sees a reef. Coral reefs rival that other great tropical community, the rain forest, in their beauty, richness, and complexity. Tropical rain forests and coral reefs are also similar in that the basic physical structure of both communities is produced by organisms. Both reef-building corals and the giant trees of a rain forest create a three-dimensional framework that is home to a vast assortment of organisms. Coral reefs are massive, in fact, they are considered not only biological communities but geological structures, the largest geological features built by organisms.

Oysters, polychaete worms, and red algae can also form reefs, and some cold-water corals slowly build mounds on the sea floor (see "Deep-Water Coral Communities, p. 317). None of these features are as widespread, as large, or as structurally complex as tropical coral reefs.

THE ORGANISMS THAT BUILD REEFS

Coral reefs are made of huge amounts of **calcium carbonate ($CaCO_3$),** or limestone, that is deposited by organisms. Of the thousands of species in coral reef communities, only a fraction produce the limestone reef. The most important of these reef-building organisms, as you might guess, are corals.

Table 14.1 Major Groups of Corals and Related Cnidarians on Coral Reefs

Common Name	Importance as Reef Builders	Notes
ANTHOZOANS (Lack medusa stage and live only as polyps; same group as sea anemones)		
Scleractinian corals	The main reef builders	Produce a calcareous skeleton; nearly all have zooxanthellae.
Soft corals	Not reef builders	Common on coral reefs (Fig. 14.28); most have zooxanthellae but do not produce a rigid calcareous skeleton.
Organ-pipe corals (*Tubipora*)	Minor	Named for pipe-like structure of skeleton; have zooxanthellae and produce a calcareous skeleton.
Blue coral (*Heliopora*)	Significant in some places	Named for distinct blue color of skeleton; has zooxanthellae and produces a calcareous skeleton.
Gorgonians	Not reef builders	Sea fans (Fig. 7.11) and sea whips; hard skeleton is made mostly of protein and not calcareous; some have zooxanthellae.
Precious corals		Gorgonians with a pink, red, or gold calcareous skeleton used for jewelry; occur mainly in deep water rather than on coral reefs and do not contribute to reef growth; lack zooxanthellae.
Black corals	Not reef builders	Used to make jewelry and sometimes called "precious corals" but are a different group from gorgonian precious corals; hard skeleton is made of protein and is not calcareous; commonly occur in deep and cold surface waters as well as on coral reefs.
HYDROZOANS (Have both medusa and polyp stages but are seen on reef only as polyps; same group as jellyfishes)		
Fire corals (*Millepora*)	Significant in some places	Named because touching them produces a burning sensation from their powerful nematocysts; have zooxanthellae and produce a calcareous skeleton.
Lace corals (*Stylaster*)	Insignificant	Named for delicate, branched colonies; lack zooxanthellae but produce a calcareous skeleton; commonly occur in deep and cold surface waters as well as on coral reefs.

Reef Corals

"Coral" is a general term for several different groups of **cnidarians,** only some of which help build reefs (Table 14.1). In reef-building, or **hermatypic,** corals the **polyps** produce calcium carbonate skeletons. Billions of these tiny skeletons form a massive reef. The most important reef builders are a group known as **scleractinian corals,** sometimes called the stony or "true" corals.

Nearly all reef-building corals contain symbiotic **zooxanthellae** (Fig. 14.1) that help the corals make their calcium carbonate skeletons. Corals can produce their skeletons without zooxanthellae but only very slowly, not nearly fast enough to build a reef. It is the zooxanthellae as much as the corals themselves that construct the reef framework, and without zooxanthellae there would be no reefs. Corals that do not help build reefs, or **ahermatypic** corals, often lack zooxanthellae.

The primary architects of coral reefs are reef-building corals that produce calcium carbonate skeletons with the help of symbiotic zooxanthellae.

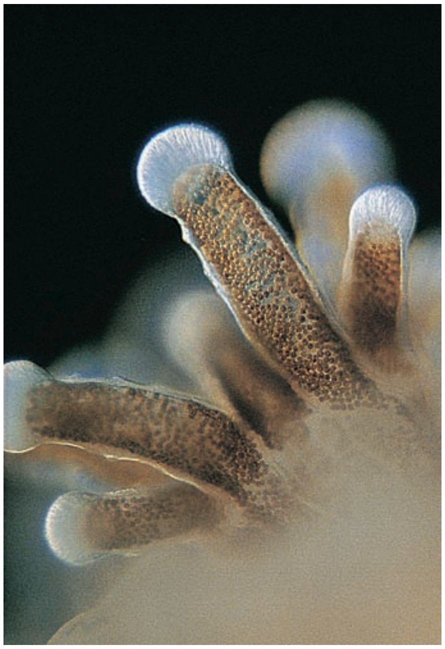


FIGURE 14.1 The microscopic, golden-brown zooxanthellae that pack these polyp tentacles help corals build reefs. They also occur in giant clams, some sea anemones (see Fig. 11.26), and other invertebrates. Cells in the white, bulbous tips of the tentacles are packed with nematocysts.

The Coral Polyp You have to look closely to see the little polyps that build coral reefs. Coral polyps are not only small but deceptively simple in appearance. They look much like little sea anemones, consisting of an upright cylinder of tissue with a ring of tentacles on top (Figs. 14.2 and 14.3*b*). Like anemones and other cnidarians, they use their nematocyst-armed tentacles to capture food, especially zooplankton. The tentacles surround the mouth, the only opening to the sac-like gut.

Most reef-building corals are colonies of many polyps, all connected by a thin sheet of tissue. The colony starts when a planktonic coral larva, called a **planula,** settles on a hard surface. Coral larvae generally do not settle on soft bottoms. The larva transforms, or **metamorphoses,** into a single "founder" polyp that, if it survives, divides over and over to form the colony. The digestive systems of the polyps usually remain connected, and they share a common nervous system (Fig. 14.4). A few reef-building corals consist of only a single polyp (Fig. 14.3*a*).

Coral polyps lie in a cup-like skeleton of calcium carbonate that they make themselves. The polyps continually lay down new layers of calcium carbonate, building up the skeleton beneath them so that it grows upward and outward (Fig. 14.5). The skeleton forms nearly all the bulk of the colony (Fig. 14.6) and can take many different shapes (Fig. 14.7). The actual living tissue is only a thin layer on the surface. It is the calcareous coral skeletons that form the framework of the reef.

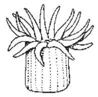
Coral Nutrition Zooxanthellae nourish the host coral as well as help it deposit its skeleton. They perform **photosynthesis** and pass some of the organic matter they make on to the coral (Fig. 14.8). Thus, the zooxanthellae feed the coral from the inside. Many corals can survive and grow without eating, as long as the zooxanthellae have enough light.

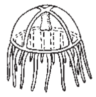
Although corals get much of their nutrition from their zooxanthellae, most eat when they get the chance. They prey voraciously on zooplankton. The billions of coral polyps on a reef, along with all the other hungry reef organisms, are very efficient at removing zooplankton brought in by currents. Indeed, the reef has been called a "wall of mouths."

Coral polyps catch zooplankton and **detritus** with their tentacles or in sheets of mucus that they secrete on the colony surface. Tiny, hair-like cilia gather the mucus into threads and pass them along to the mouth. Some corals hardly use their tentacles and rely on the mucus method. A few have even lost tentacles altogether.

Corals have still other ways of feeding themselves. There are a number of long, coiled tubes called **mesenterial filaments** attached to the wall of the gut (see Fig. 14.2). The mesenterial

Cnidarians Animals in the phylum Cnidaria; they have radial symmetry, tissue-level organization, and tentacles with *nematocysts,* specialized stinging structures.
Life stages of cnidarians:
Polyp The sessile, sac-like stage, with the mouth and tentacles on top.
Medusa The swimming, bell-like stage, with the mouth and tentacles underneath.
- Chapter 7, p. 119





Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Zooxanthellae Dinoflagellates (single-celled, photosynthetic algae) that live within animal tissues.
- Chapter 5, p. 96

Symbiosis The living together in close association of two different species, often divided into *parasitism,* where one species benefits at the expense of the other; *commensalism,* where one species benefits without affecting the other; and *mutualism,* where both species benefit.
- Chapter 10, p. 218

Photosynthesis

$$CO_2 + H_2O + \text{sun energy} \rightarrow \underset{\text{(glucose)}}{\text{organic matter}} + O_2$$

- Chapter 4, p. 66

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

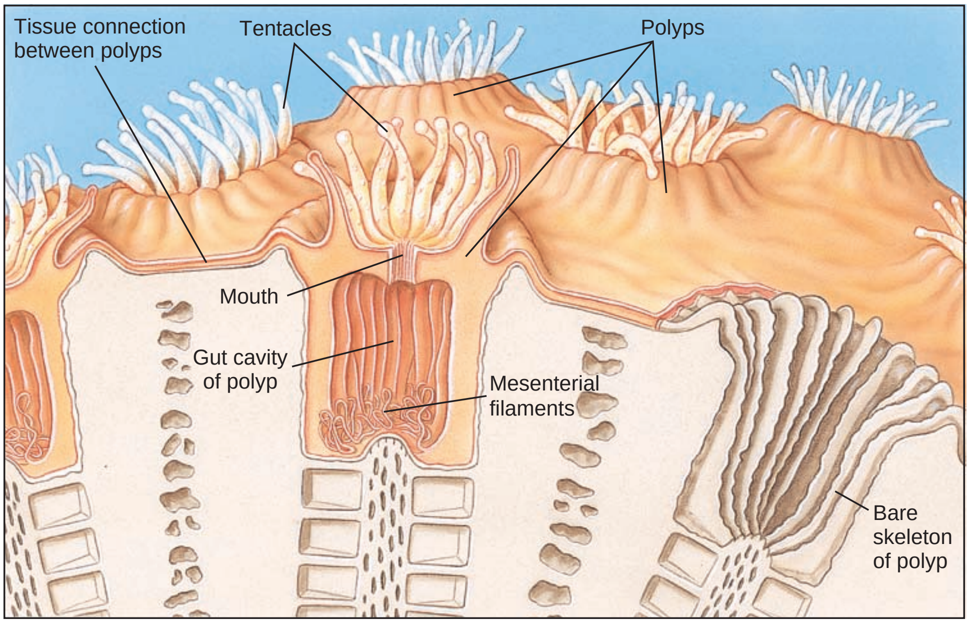
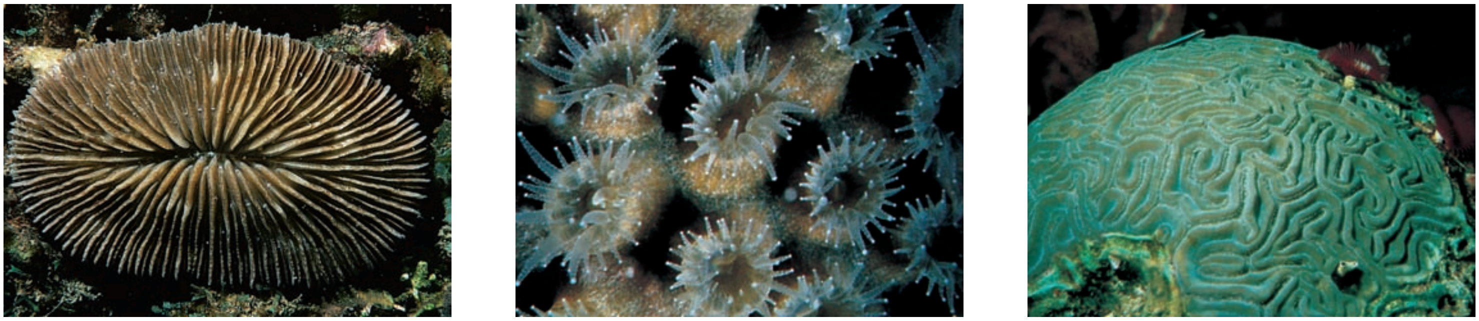


FIGURE 14.2 Cutaway view of one of the polyps in a coral colony and of the calcium carbonate skeleton underneath. The polyps are interconnected by a very thin layer of tissue.



(a) (b) (c)

FIGURE 14.3 Coral polyps. (*a*) A few corals consist of a single polyp, which as in this mushroom coral (*Fungia*) may be free-living, or not attached to the bottom. Most corals are colonies of many individual polyps. (*b*) In some of these, like the large-cupped boulder coral (*Montastrea cavernosa*) from the Caribbean, each polyp has its own individual cup, called a corallite. (*c*) In coral colonies like this brain coral (*Diploria*) from the Caribbean, meandering lines of polyps lie in a common corallite.

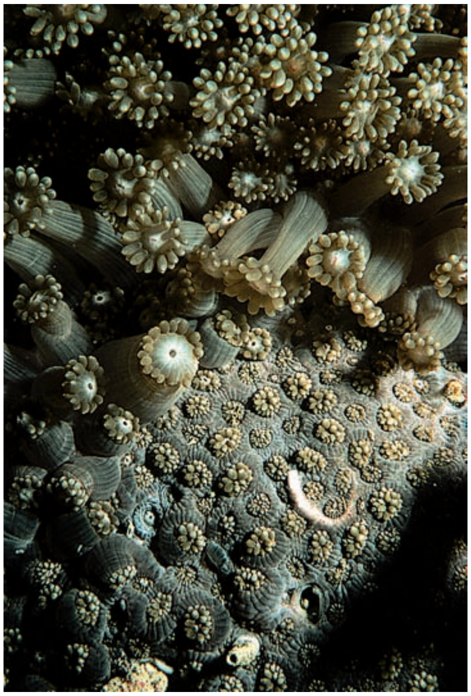


FIGURE 14.4 The polyps in a coral colony are interconnected. If you touch an extended polyp, it will contract, and so will its neighbors, followed by their neighbors, and so on, so that a wave of contraction passes over the colony. In this colony of the coral *Goniopora lobata* the wave of contraction is moving up from the bottom.

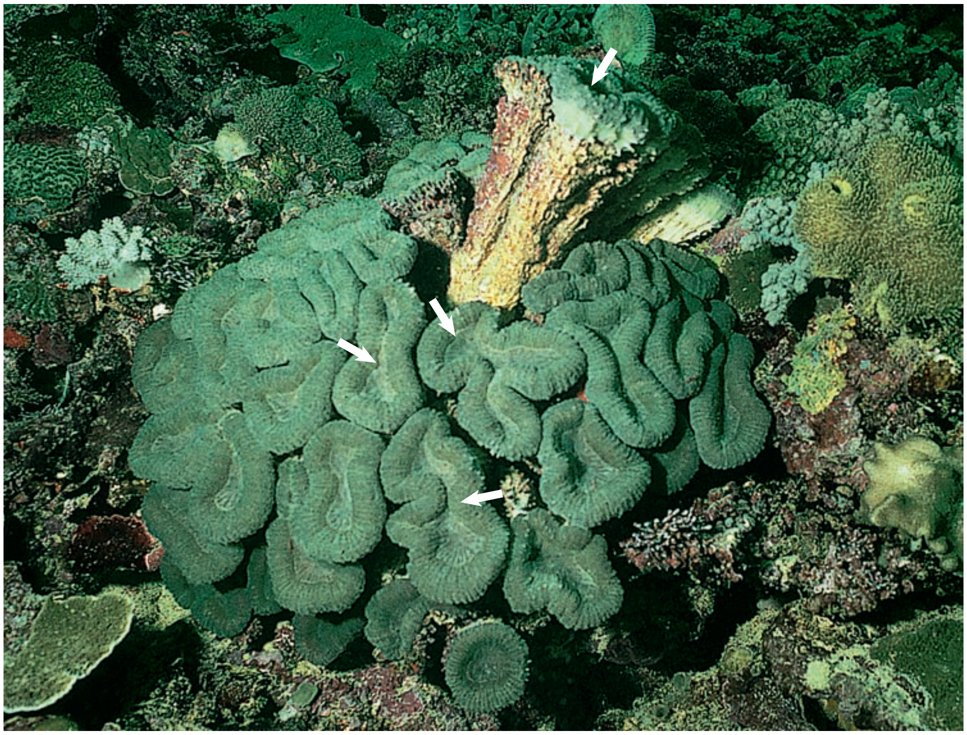


FIGURE 14.5 This coral (*Lobophyllia hemprichii*) shows particularly well how corals build up their skeleton. Each of the irregular rings (arrows) is a single polyp that has built up a column of calcium carbonate skeleton.

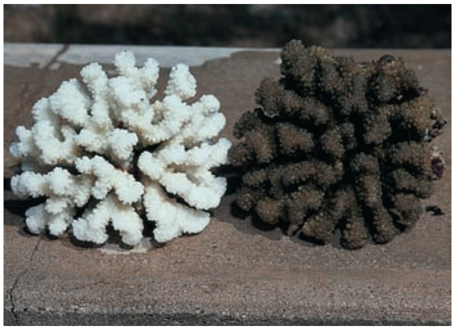


FIGURE 14.6 The calcium carbonate skeleton makes up most of a coral colony. A live colony (*Pocillopora verrucosa*) is shown on the right. On the left is a colony with the living tissue removed. The main difference is the color; the live part is only a thin layer of tissue on the surface. The "corals" sold in shell and aquarium shops are actually only the skeletons of live corals that were taken from the reef and bleached. Some reefs have been devastated by the collectors who supply these shops in order to feed their families.

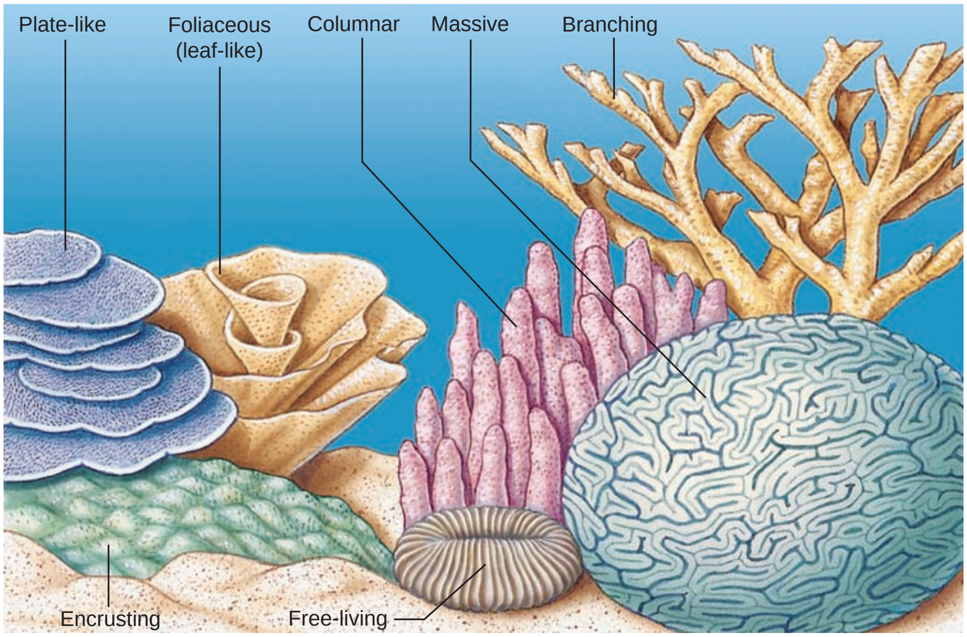


FIGURE 14.7 Corals come in a multitude of shapes, or growth forms.

filaments secrete digestive enzymes. The polyp can extrude the filaments through the mouth or body wall to digest and absorb food particles outside the body. Corals also use the mesenterial filaments to digest organic matter from the sediments. In addition, corals can absorb **dissolved organic matter (DOM)** (see "The Trophic Pyramid," p. 223).

Corals nourish themselves in a remarkable number of ways. Zooxanthellae are the most important source of nutrition. Corals can also capture zooplankton and detritus with tentacles or mucus nets, digest organic material outside the body with mesenterial filaments, or absorb dissolved organic matter (DOM) from the water.

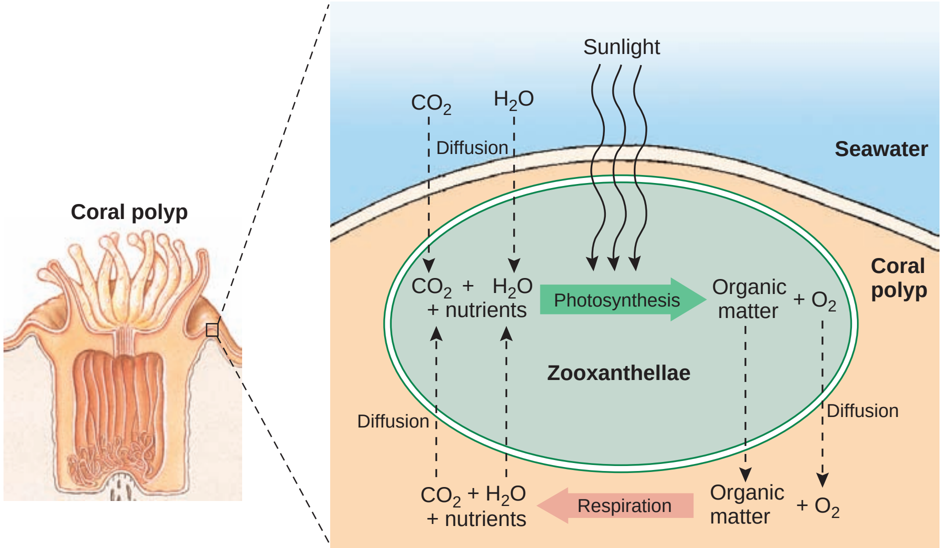


FIGURE 14.8 Zooxanthellae in a coral's tissue perform photosynthesis and transfer some of the organic matter they manufacture to the coral host. Carbon dioxide and nutrients are continually recycled between the coral and its zooxanthellae.

Other Reef Builders

Although they are the chief architects, corals cannot build a reef alone. Many other organisms help. The most important of these are algae, which are essential to reef growth. In fact, some marine biologists prefer to call coral reefs "algal reefs" or "biotic reefs." One reason for this is that zooxanthellae, which are algae, are essential to the growth of corals. There are other algae, however, that also have key roles in building the reef. Encrusting **coralline algae** (*Porolithon, Lithothamnion*) grow in rock-hard sheets over the surface of the reef. They deposit considerable amounts of calcium carbonate, sometimes more than corals, and thus contribute to reef growth. Coralline algae are more important on Pacific reefs than Atlantic ones.

Encrusting coralline algae help not only to build the reef but also to keep it from washing away. The stony pavement formed by these algae is tough enough to withstand waves that would smash even the most rugged corals. The algae form a distinct ridge on the outer edge of many reefs, especially in the Pacific. This **algal ridge** absorbs the force of the waves and prevents erosion from destroying the reef.

Encrusting algae do yet another job that is vital to reef growth. Coral skeletons and fragments create an open network, full of spaces, that traps coarse carbonate sediments (Fig. 14.9). Sediment, especially fine sediment, damages corals when it settles directly on them, but the buildup of coarse sediment in the reef framework is an essential part of reef growth. The structure of a reef is formed as much by the accumulation of calcareous sediment as by the growth of corals. Encrusting algae grow over the sediment as it builds up, cementing the sediment in place. Thus, encrusting coralline algae are the glue that holds the reef together. Some invertebrates, notably sponges and **bryozoans,** also help bind the sediments.

Encrusting coralline algae help build the reef by depositing calcium carbonate, by resisting wave erosion, and by cementing sediments.

Nearly all the sediment that accumulates to help form the reef comes from corals and the shells or skeletons of other organisms. In other words, nearly all the sediment is **biogenous. Coral rubble,** fragments of broken coral, is one important source of sediment on reefs. Another important sediment-forming organism is a calcareous green alga called *Halimeda* (Fig. 14.10). *Halimeda* deposits calcium carbonate within its tissues to provide support and discourage grazers—a mouthful of limestone is pretty unappetizing. The remnants of *Halimeda* accumulate on reefs in huge amounts, to be bound together by encrusting organisms.

Many other organisms make calcium carbonate sediments and thus contribute to the growth of the reef. The shells of **forams,** snails, clams, and other molluscs are very important. Sea urchins, bryozoans, crustaceans, sponges, bacteria and a host of other organisms add or help bind carbonate sediments. Reef growth is truly a team effort.

The accumulation of calcium carbonate sediments plays an important role in reef growth. A calcareous green alga, *Halimeda,* and coral rubble account for most of the sediment, but many other organisms also contribute.

A great deal of the sediment on reefs comes from the activities of organisms that do not deposit calcium carbonate themselves but instead break down the solid reef structure. Many animals scrape or bite their food off the reef with some sort of hard structure. Parrotfishes, for example, are named for their fused teeth that form a parrot-like beak (see Fig. 8.13*d*). Sea urchins scrape algae off the reef with their **Aristotle's lantern.** In the process, these and many other grazers remove bits of calcium carbonate from the reef to form sediment. The erosion caused by such organisms, or **bioerosion,** tends to wear the reef away, although some of the sediment they create does get reincorporated into the reef structure. Many

Coralline Algae Red algae that deposit calcium carbonate ($CaCO_3$) in their tissues.
- Chapter 6, p. 107

Bryozoans Small, colonial, encrusting animals that make delicate, often lace-like, skeletons.
- Chapter 7, p. 140; Figure 7.42

Foraminiferans (Forams) Protozoans, often microscopic, with a calcium carbonate shell.
- Chapter 5, p. 97; Figure 5.11

Aristotle's Lantern A complicated set of calcium carbonate ($CaCo_3$) teeth and associated muscles that is found in sea urchins.
- Chapter 7, p. 143

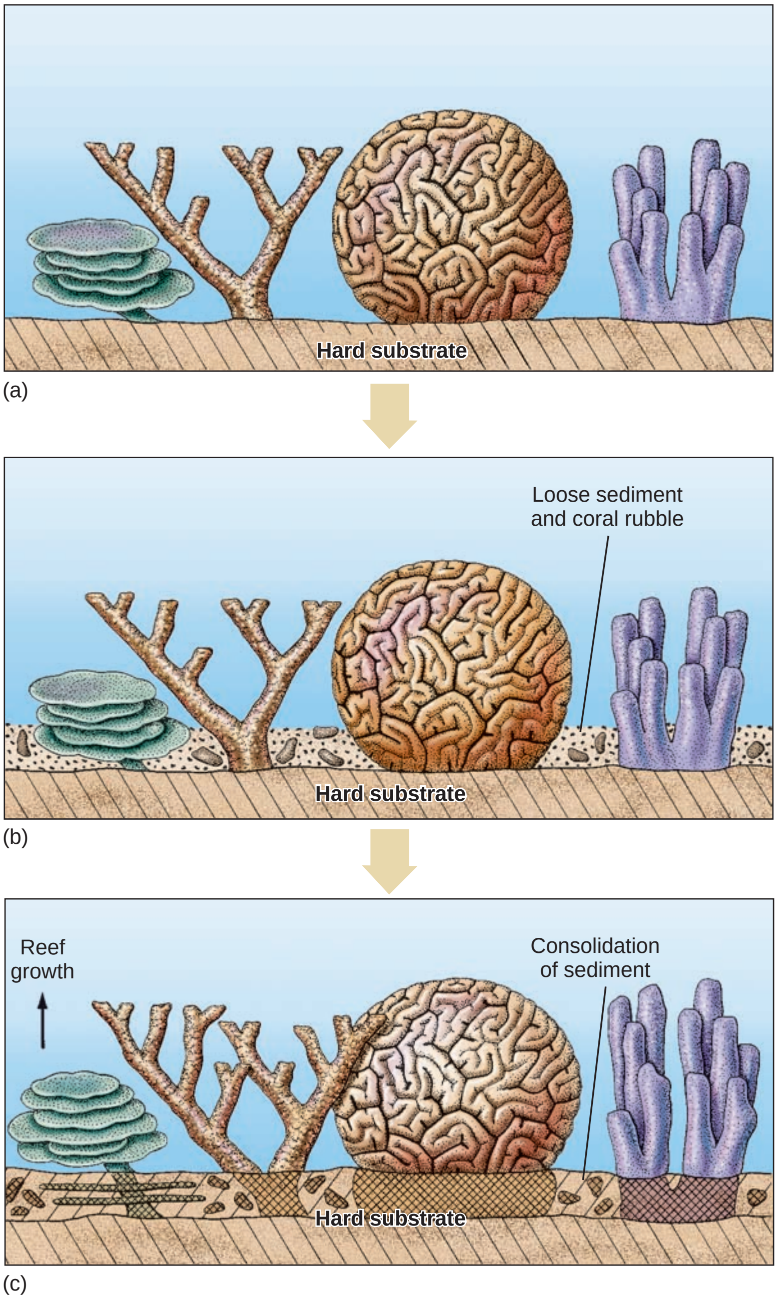


FIGURE 14.9 Reef growth involves several processes. (*a*) The framework is made when reef-building corals settle and grow on some hard surface, usually a preexisting reef. (*b*) The spaces in this framework are partially filled in by coarse carbonate sediments. (*c*) When the sediments are glued together by encrusting organisms, new reef "rock" is formed and the reef has grown. On a real reef all three steps go on at the same time. Reefs are not actually completely solid as depicted here but are porous, with many holes and crevices that serve as home to a multitude of organisms.

other organisms—including sponges, clams, polychaete and other worms, and algae—cause bioerosion by burrowing into or through the reef limestone, either scraping it away to form sediment or dissolving it. A reef grows only if corals, coralline algae, and sediment-forming and -binding organisms accumulate limestone faster than the bioeroders wear it away.

Bioeroders have another important role in reef communities. Their burrowing creates spaces in the reef framework, nooks and crannies where other organisms can hide. More species live inside the reef framework, in fact, than on its surface.

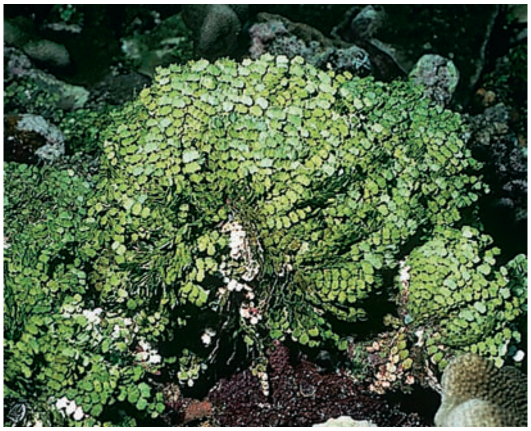


FIGURE 14.10 This calcareous green alga (*Halimeda*) is one of the main sediment-forming organisms on most reefs. About 95% of the plant's weight is calcium carbonate, and there is only a thin layer of live tissue on the outside. When the tissue dies the segments separate, each leaving a piece of limestone.

Conditions for Reef Growth

Other organisms may be important, but coral reefs do not develop without reef-building corals. Corals have very particular requirements that determine where reefs develop. Reefs are rare on soft bottoms, for example, because coral larvae need to settle on a hard surface.

Light and Temperature Corals can grow only in shallow water, where light can penetrate, because the zooxanthellae on which they depend need light. Calcareous algae require sunlight, too. Particular types of coral and algae have different depth limits—some can live deeper than others—but reefs rarely develop in water deeper than about 50 m (165 ft). Because of this, coral reefs are found only on the continental shelves, around islands, or on top of seamounts. Many types of coral live in deep water and do not need light, but these corals do not contain zooxanthellae or build massive reef structures (see "Deep-Water Coral Communities," p. 317). Corals also often prefer clear waters, since water clouded with sediment or plankton reduces light penetration.

Reef-building corals are limited to warm water and can grow and reproduce only if the average water temperature is above about 20°C (68°F). Most reefs grow in considerably warmer areas. Figure 14.11 illustrates the relationship between coral reefs and water temperature.

Corals need light and warm temperatures, so reefs grow only in shallow, warm waters.

Water that is *too* warm is also bad for corals. The upper temperature limit varies, but is usually around 30° to 35°C (86° to 95°F). The first outward sign of heat stress, or stress of other kinds, is **bleaching,** in which the coral expels its zooxanthellae (see Fig. 18.3). It is called bleaching because the golden-brown or greenish zooxanthellae give corals most of their color; without zooxanthellae the coral's tissue is almost transparent and the coral looks white because of its underlying limestone skeleton. Corals also slough off large amounts of slimy mucus when stressed. Corals

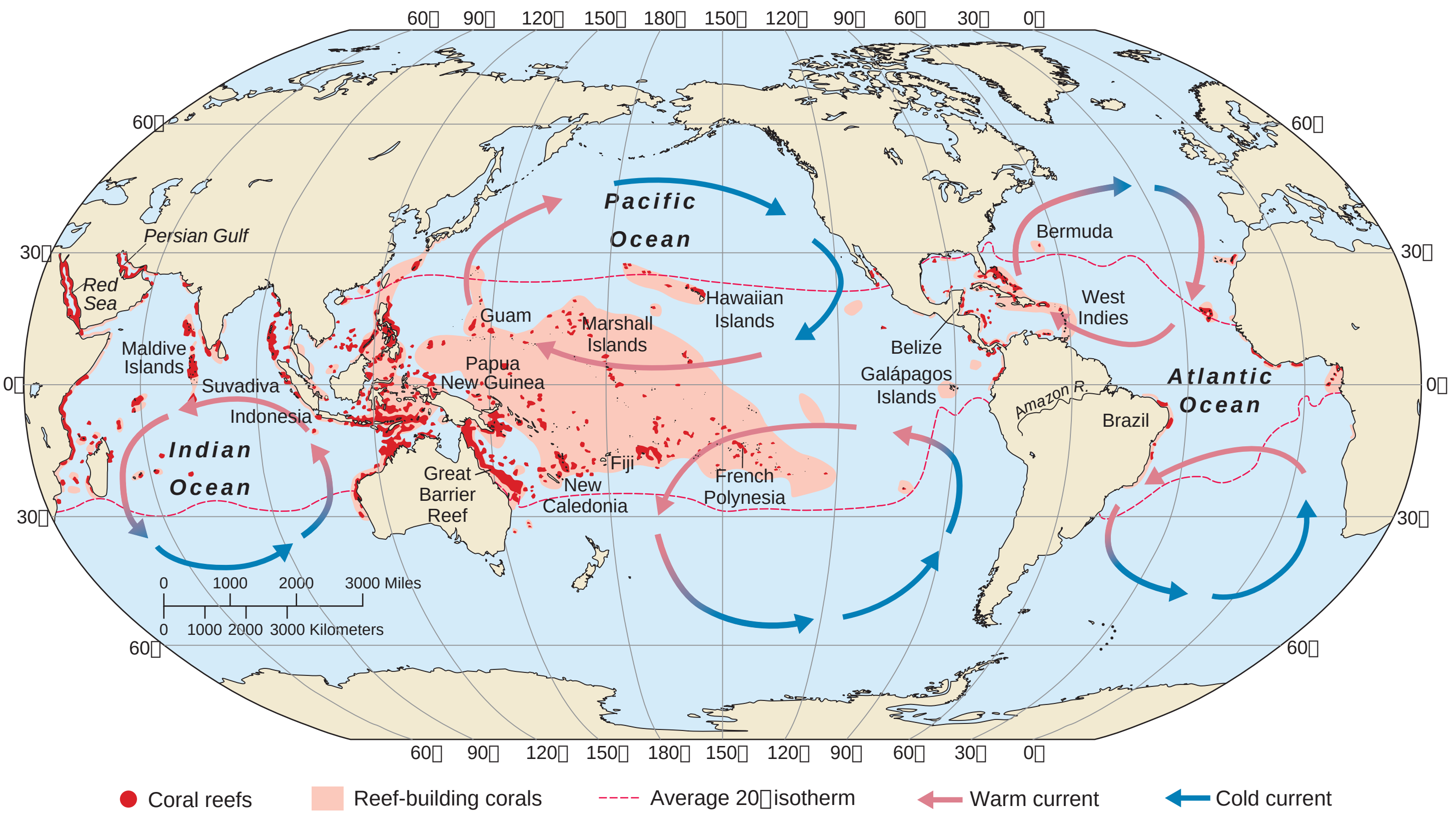

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60°
30°
0°
30°
60°
Pacific Ocean
Persian Gulf
Red Sea
Maldive Islands
Suvadiva
Indonesia
Indian Ocean
Guam
Marshall Islands
Hawaiian Islands
Papua New Guinea
Great Barrier Reef
Fiji
New Caledonia
French Polynesia
Belize
Galápagos Islands
Bermuda
West Indies
Amazon R.
Brazil
Atlantic Ocean
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
Coral reefs
Reef-building corals
Average 20° isotherm
Warm current
Cold current

FIGURE 14.11 The distribution of reef coral communities, including those that do not form structural reefs. Note that the distribution of reef corals, like that of kelps, is related to temperature. Reef corals require warm water, however, while kelps need cold water. Compare the distribution of reefs with that of kelps shown in Figure 13.21. Note that because of warm surface currents corals extend further north and south on the east sides of continents than on the west sides.

often recover from bleaching, regaining their symbionts either from the regrowth of the few that remain or by acquiring new ones from the water. If the warm conditions last too long or the temperature gets too high, however, the coral dies.

Temperature limits vary among coral species and from place to place. Corals from warm locations, for example, tolerate higher temperatures than corals from cooler waters (Fig. 14.12). Corals can also adapt to fluctuating conditions. For instance, reefs grow in parts of the Persian Gulf where the water temperature ranges from 16° to 40°C (60° to 104°F). The symbiotic zooxanthellae, different species and strains of which vary in their temperature tolerances, may be partly responsible for this temperature adaptation. Bleaching may occur simply because one partner or the other is weakened or damaged by stress, or be caused by viruses or other disease-causing organisms. There is also evidence that corals may bleach to expel zooxanthellae that are poorly adapted to high temperature in order to acquire better-adapted symbionts, though this hypothesis is controversial.

In any case, the upper thermal tolerances of corals are usually not far above the normal temperature range where they live. Corals suffer when exposed to temperatures outside this normal range. This sometimes happens during extreme low tides, when shallow pools on the reef may be cut off from circulation. Heated by the sun, the water can warm up to fatal temperatures. By discharging heated water, power plants can also kill corals.

El Niño (see "The El Niño–Southern Oscillation Phenomenon," p. 353), brings unusually warm water to many parts of the ocean. Widespread coral bleaching and mortality also occur during El Niño events. During the unusually strong El Niño of 1997–98, severe bleaching occurred on many reefs around the world, probably as a direct result of the unusually warm water. In some places, including the Caribbean and parts of the Great Barrier Reef, bleaching did not kill many corals, and reefs quickly recovered after the water cooled. In other areas, such as the Indian Ocean, Southeast Asia, and the far western Pacific, many corals died after bleaching and some reefs were severely damaged. Many of these reefs have recovered slowly or not at all.

High water temperatures have led to other, more localized, bleaching events almost every year since the 1997–98 El Niño. Reef scientists are increasingly concerned that bleaching is becoming more frequent and more intense as a result of global climate change (see "What's Happening Now," p. 233). We must remember that coral bleaching and El Niño are natural events, and some of the apparent increase in bleaching may just reflect the fact that bleaching is much more likely to be reported now than in the past. Temperature records stored in oxygen isotopes of fossil corals, in fact, indicate that the strongest El Niño events of the past millennium probably occurred in the mid-17th century, long before the industrial revolution began intensifying the greenhouse effect. Widespread coral bleaching probably followed, but there aren't any scientific records of it.

Nevertheless, the sea has steadily warmed over the last 50 to 100 years, exposing reefs more and more often to stressful temperatures, and global warming will continue. Coupled with ocean acidification, pollution, and other human-induced stresses (see

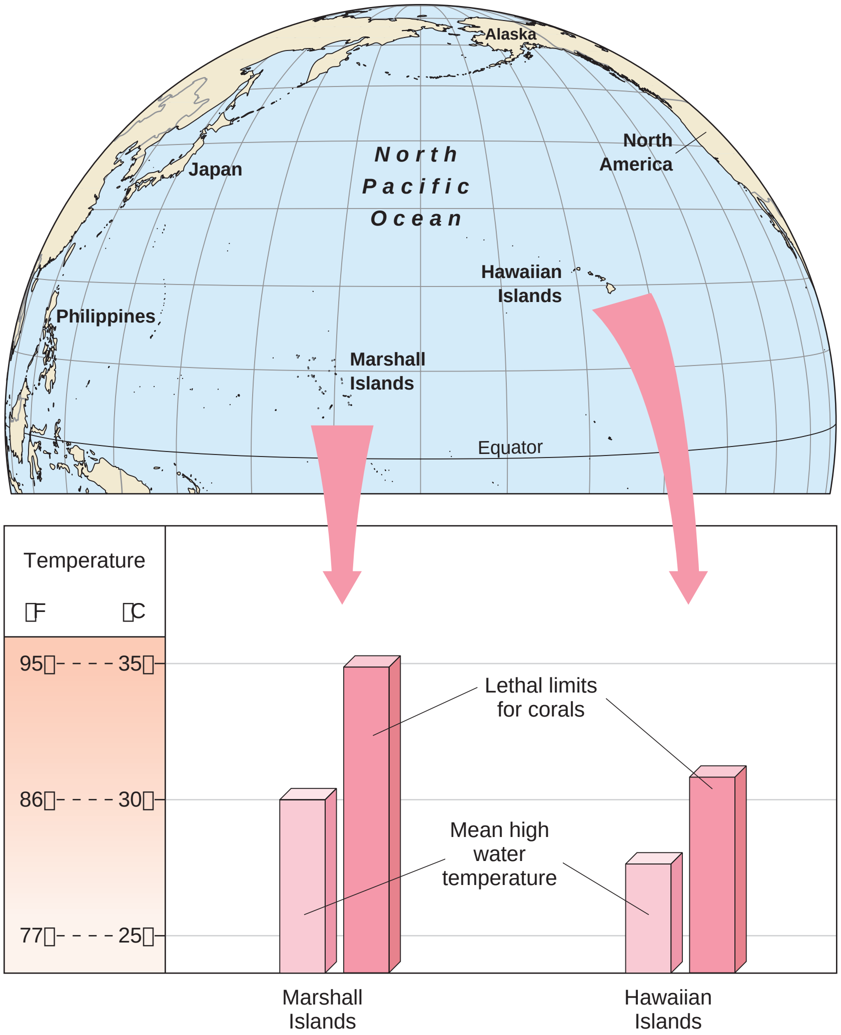


FIGURE 14.12 The upper temperature limit of corals is related to the temperature at their home sites. For example, the water in the Marshall Islands is warmer on average than that in Hawai‘i. During the hottest months of the year the average high temperature is several degrees higher in the Marshalls. Corals from the Marshalls can tolerate correspondingly higher temperatures. Why do you think the highest temperature that the corals can tolerate would be higher than the average high temperature at their location?

“Coral Reefs, p. 403), many scientists fear for the future of the world’s reefs.

Salinity, Sediments, and Pollution Most corals are quite sensitive to reduced salinity and do not do well near river mouths, for example, where there is a lot of freshwater input. This is not only because of the lowered salinity but also because rivers bring in a lot of silty sediment, which is generally unfavorable to corals. It clouds the water, cutting down light for the zooxanthellae. Sediment on the colony surface can smother the coral or cause disease, though the coral can clean itself to some extent by sloughing off mucus that carries the sediment away.

Some corals do thrive in silty environments and even feed on organic-rich sediment particles. Most reefs, however, develop in clear, low-sediment waters and are vulnerable to high levels of sediment unless there is enough wave or current action to wash the sediment away (Fig. 14.13). Many reefs around the world have been damaged by human activities like mining, logging, construction, and dredging that greatly increase the flow of sediment onto the reef.

Corals are also sensitive to pollution of many kinds. Even low concentrations of pesticides and industrial wastes can harm them. Larvae are especially sensitive. In high concentrations, nutrients, too, can be harmful. Humans release tremendous amounts of nutrients in sewage and in fertilizers that are washed from farmland to the sea. The nutrients may harm the corals directly by interfering with the formation of their skeletons. More importantly, increased nutrients can alter the ecological balance of the community. Most coral reefs grow in water that is naturally low in nutrients. In such nutrient-poor water, seaweeds do not grow very rapidly and are kept under control by grazers. This allows corals to compete successfully for space and light. When nutrients are added, seaweeds may grow much faster and shade and choke out the slow-growing corals. This is a particular problem when, as is often the case, fishing has reduced populations of grazing fishes and other organisms.

Corals are very sensitive to fresh water, fine sediment, and pollution, including pollution by high nutrient levels.

The Kāne‘ohe Bay Story One of the best-known examples of the harmful effects of nutrient enrichment occurred in a partially enclosed bay in the Hawaiian Islands. Kāne‘ohe Bay, located on the northeast shore of the island of O‘ahu, once had some of the most luxuriant reefs in Hawai‘i. Until the 1930s the area around the bay was sparsely populated. In the years leading up to World War II, with the military buildup of O‘ahu, the population began to increase. This increase continued after the war as the shores of the bay were developed for residential use.

Treated sewage from this expanding population was discharged into the bay. By 1978 about 20,000 m^3 (over 5 million gallons) of sewage were entering the bay every day. Long before then, by the mid-1960s in fact, marine biologists began to notice disturbing changes in the middle part of the bay. Loaded with nutrients, the sewage acted as a fertilizer for seaweeds. A green alga, the bubble alga (*Dictyosphaeria cavernosa*), found the conditions particularly to its liking and grew at a tremendous rate, literally covering the bottom in many parts of the bay. Bubble algae began to overgrow and smother the corals. Phytoplankton also bloomed, clouding the water. Kāne‘ohe Bay’s reefs began to die. Such accelerated algal growth due to nutrient input is called **eutrophication** (see “Eutrophication,” p. 405).

For a time it seemed that the story had a happy ending. As the once beautiful reefs smothered, scientists and the general public cried out. It took a while, but in 1978 public pressure finally forced the diversion of the treated sewage offshore, greatly reducing nutrient input to the bay. The result was dramatic. Bubble algae died back in much of the bay, and the bay’s corals began to recover much faster than anyone expected. By the early 1980s, bubble algae were fairly scarce and corals had started to grow again. The reefs were not what they once were but seemed to be on track to recover.

Coral Reproduction

Corals are amazingly adaptable animals. They come in all shapes and sizes and have many ways to feed themselves. It should come as no surprise, then, that they also have more than one way to reproduce.

One form of reproduction in corals is essentially the same as growth. As individual polyps reproduce vegetatively by dividing into new polyps, the colony as a whole grows. The process is taken a step further when a piece of a coral colony breaks off and grows into a new "daughter" colony. This reproduction by fragmentation seems to be quite important for some coral species, which may even be adapted to break easily to produce more fragments. The growth of broken coral fragments into new colonies can be an important part of the recovery of reefs from storm damage and other disturbances, and transplanting fragments is one way that scientists and conservation groups help restore damaged reefs (see "Restoration of Habitats," p. 417). Some corals, especially free-living ones, reproduce asexually by budding (see Fig. 4.19*a*).

Corals also reproduce sexually. They produce eggs and sperm, which fuse and develop into planulae, the characteristic larvae of cnidarians. Some coral species have separate sexes, but about 75% are hermaphrodites and make both eggs and sperm. The method of fertilization also varies. In some corals, whether or not they are hermaphrodites, the egg is fertilized and develops inside the polyp. Most corals, however, are broadcast spawners and release eggs and sperm into the water.

The most spectacular form of sexual reproduction in corals is mass spawning, in which many different coral species on a reef all spawn at the same time. Mass spawning was first reported from the Great Barrier Reef, where it takes place for a few nights a year between October and early December just after a full moon. At a given place the time of the mass spawning event can usually be predicted down to the night. Since its discovery on the Great Barrier Reef mass spawning has been observed on many other reefs around the world.

Spawning corals release their eggs and sperm through the mouth. In some species the gametes are packaged in little bundles, which may contain both eggs and sperm or only one or the other. The bundles float to the surface and break up, allowing the eggs and sperm to mix.

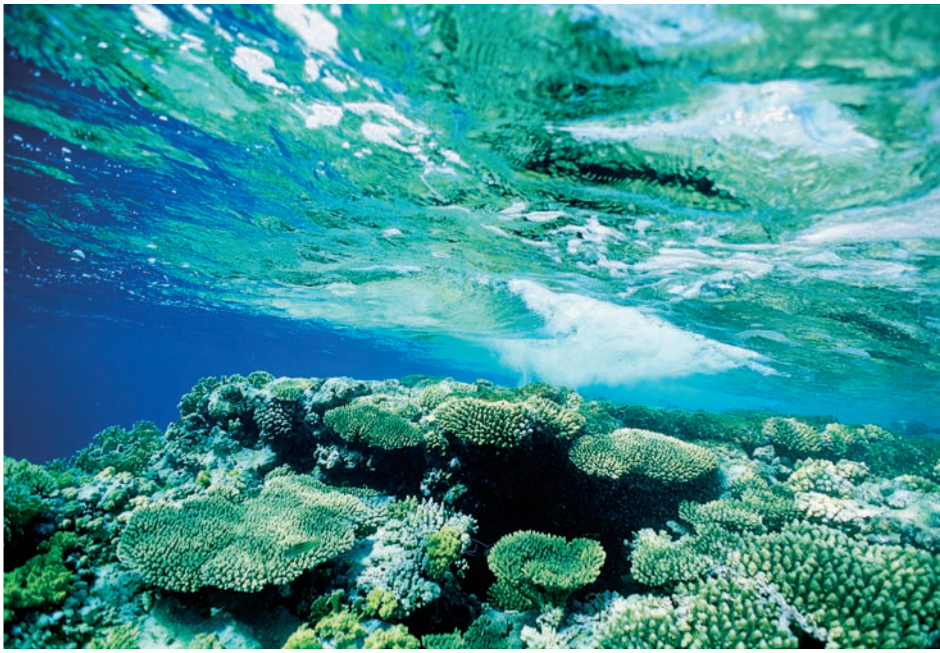
Nobody knows why the corals all spawn together. Maybe egg predators get so full that most of the eggs go uneaten. It might have something to do with the tides. There may be an explanation that no one has thought of. Another interesting thing is that although mass spawning happens on some reefs it doesn't occur on others. Is there something different about these reefs? Finding answers to these questions is likely to occupy coral biologists for some time to come.

The release of sperm and egg bundles during the mass coral spawning on the Great Barrier Reef. Photographs coutresy of the Great Barrier Reef Marine Park Authority.

Then the ghost of pollution past reared its ugly head. In November 1982, Hurricane Iwa struck Kāneʻohe Bay. Layers of the coral skeleton that formed during the years of pollution were weakened, becoming fragile and crumbly. When the hurricane hit, this weak layer collapsed and many reefs were severely damaged. Fortunately, the corals were already beginning to recover, and the broken pieces were able to grow back. If the hurricane had hit during the years of pollution, the reefs of Kāneʻohe Bay—and their benefits to fishing, tourism, and recreation—might have disappeared forever.

The rapid recovery of Kāneʻohe Bay's reefs that was seen during the early 1980s did not continue. By 1990 the recovery seemed to have leveled off. Some areas even began to decline again, with bubble algae once more becoming abundant. There are a number of possible explanations. Even though most sewage is now discharged outside the bay, some nutrients continue to enter from boats, the septic tanks and cesspools of private homes, and other sources. Not only that, nutrients from the old sewage outfalls were stored in the sediments, and are still being released even after 30 years. There is also evidence that fishing has reduced

FIGURE 14.13 Corals often flourish where there is plenty of wave action. The water motion keeps sediment from settling on the corals and brings in food, oxygen, and nutrients.



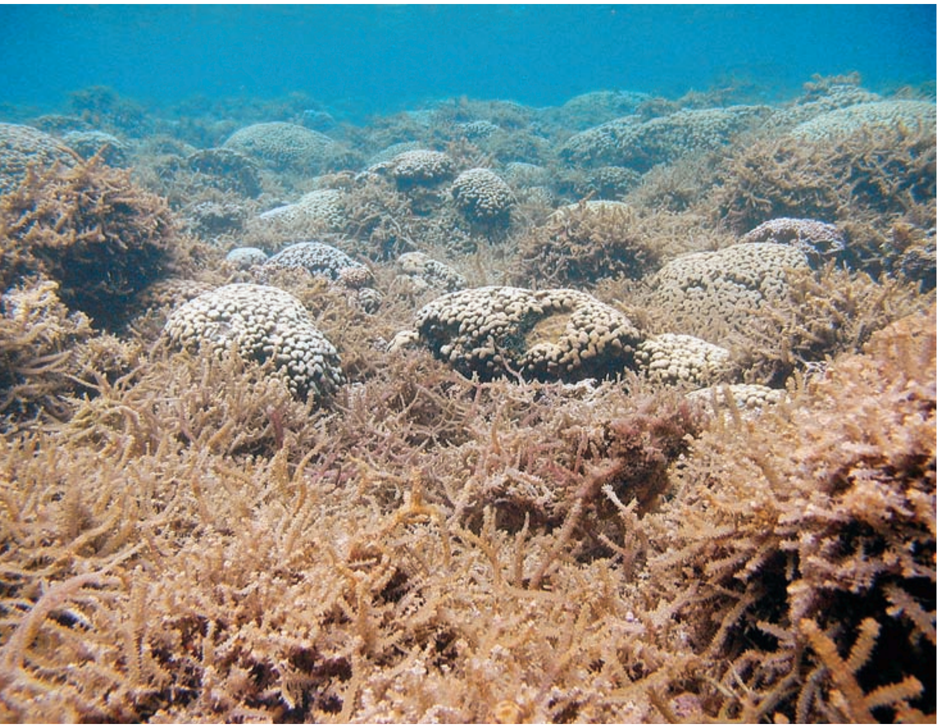


FIGURE 14.14 The red alga *Eucheuma denticulatum* is one of several species of red alga introduced to Kāneʻohe Bay for experimental mariculture that have gotten out of control. The algae are overgrowing and smothering corals in many parts of the bay.

populations of fishes that graze on bubble algae. Furthermore, the grazing fishes that remain prefer to eat other species of seaweed that have been introduced from outside Hawaiʻi and have shifted away from eating bubble algae. Thus, bubble algae may be abundant because they are not being eaten as fast as they once were. Invasive seaweeds, which like bubble algae are not preferred foods of herbivorous fishes, have also started to proliferate and smother corals in the bay (Fig. 14.14). It will be much harder to restore the coral gardens of Kāneʻohe Bay than it was to degrade them.

The Kāneʻohe Bay story is far from unique. Most of the world's tropical coasts are undergoing increasing development and population growth. As a result, more and more nutrients are ending up in waters that support coral reefs, and there are many reports of reefs being threatened by eutrophication. New research, however, is showing that the effects of added nutrients on coral reefs are more complicated than we thought. Experiments indicate that algal growth is not nutrient-limited on at least some reefs. There are even suggestions that added nutrients may sometimes be good for the zooxanthellae and help corals grow faster. The overwhelming weight of evidence, though, is that eutrophication is damaging, especially when populations of algal grazers are reduced. Many reef biologists consider it one of the most serious among many threats to the world's coral reefs.

KINDS OF CORAL REEFS

Coral reefs are usually divided into three main categories: **fringing reefs, barrier reefs,** and **atolls.** Many reefs do not fit neatly into any particular category or fall between two categories. Still, the division of reefs into the three major types works well for the most part.

The three main types of reefs are fringing reefs, barrier reefs, and atolls.

Fringing Reefs

Fringing reefs are the simplest and most common kind of reef. They develop near shore throughout the tropics, wherever there is some kind of hard surface for the settlement of coral larvae. Rocky shorelines provide the best conditions for fringing reefs. Fringing reefs also grow on soft bottoms if there is even a small hard patch where corals can get a foothold. Once they get started, the corals create their own hard bottom and the reef slowly expands.

As their name implies, fringing reefs grow in a narrow band or fringe along the shore. Occurring close to land, they are especially vulnerable to sediment, freshwater runoff, and human disturbance. Under the right conditions, however, fringing reefs can be impressive. In fact, the longest reef in the world (though not the one with the largest coral area) is not the famous Great Barrier Reef in Australia but a fringing reef that runs some 4,000 km (2,500 mi) along the coast of the Red Sea. Part of the reason this reef is so well developed is that the climate is dry and there are no streams to bring in sediment and fresh water.

The typical structure of a fringing reef is shown in Figure 14.15. Depending on the place, the shore may be steep and rocky or

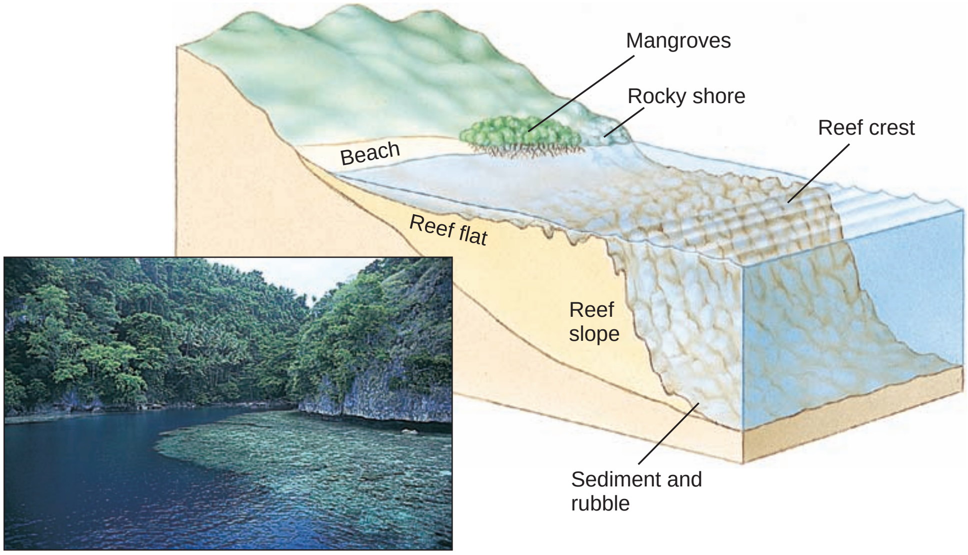


FIGURE 14.15 Typical structure of a fringing reef. Fringing reefs, like this one in the Bismarck Archipelago in the southwest Pacific (photo), can grow right up to the shore.

have mangroves or a beach. The reef itself consists of an inner **reef flat** and an outer **reef slope.** The reef flat is the widest part of the reef. It is shallow, sometimes exposed at low tide (Fig. 14.16), and slopes very gently toward the sea. Being closest to land, it is the part of the reef most strongly affected by sediments and freshwater runoff. The bottom is primarily sand, mud, or coral rubble. There are some living corals, but neither as many colonies nor as many different species as on the reef slope. Seaweeds, seagrasses, and soft corals may also occupy the reef flat, sometimes in dense beds.

The reef slope can be quite steep, vertical in fact. It is the part of the reef with the densest cover (Fig. 14.17) and the most species of coral, because the slope is away from shore and therefore away from the effects of sediment and fresh water. Also, the waves that bathe the slope provide good circulation, bring in nutrients and zooplankton, and wash away fine sediments. The **reef crest** is the shallow upper edge of the reef slope. The crest usually has even more luxuriant coral growth than the rest of the reef slope. If there is intense wave action, however, the crest may consist of an algal ridge, with the richest coral growth just below. Because there is less light in deep water, the deepest part of the reef slope usually has less live coral and fewer coral species.

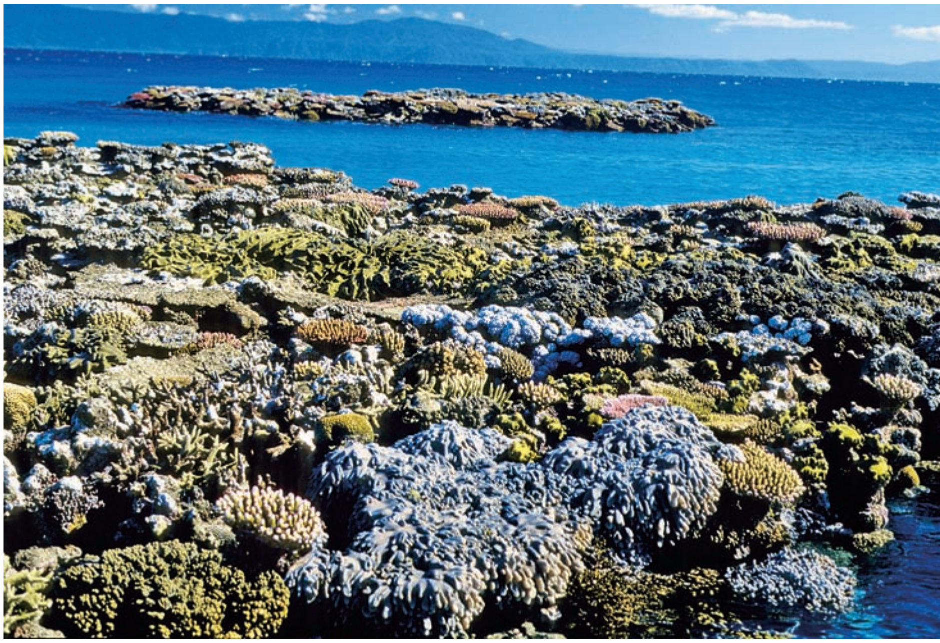


FIGURE 14.16 The upward growth of most reefs is limited by the tides. When extreme low tides occur, shallow areas like this reef flat on the Great Barrier Reef are exposed. If the corals are exposed for only a short time, they can survive, but they will die if exposed for too long. It is this occasional exposure at extreme low tides that keeps reef flats flat because all the corals above a certain depth are killed. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

Fringing reefs grow close to shore and consist of an inner reef flat and an outer reef slope.

Large amounts of sediment and coral rubble tumble down the reef slope and settle at the base. As this material builds up, reef organisms may begin to grow on it, depending on the water depth and other factors. Thus, the reef can grow outward as well as upward. Beyond the base of the slope, the bottom is usually fairly flat and composed of sand or mud. On many Caribbean reefs, turtle grass (*Thalassia testudinum*) dominates the bottom beyond the slope.

Barrier Reefs

The distinction between barrier reefs and fringing reefs is sometimes unclear because the two types grade into one another. Like fringing reefs, barrier reefs lie along the coast, but barrier reefs occur considerably farther from shore, occasionally 100 km (60 mi) or more. Barrier reefs are separated from the shore—which may also have a fringing reef—by a relatively deep **lagoon** (Fig. 14.18). Largely protected from waves and currents, the lagoon usually has a soft sediment bottom. Seagrass beds often grow in shallow parts of the lagoon. Scattered coral formations variously known as **patch reefs, coral knolls,** or **pinnacles** depending on their size and shape may grow up nearly to the surface.

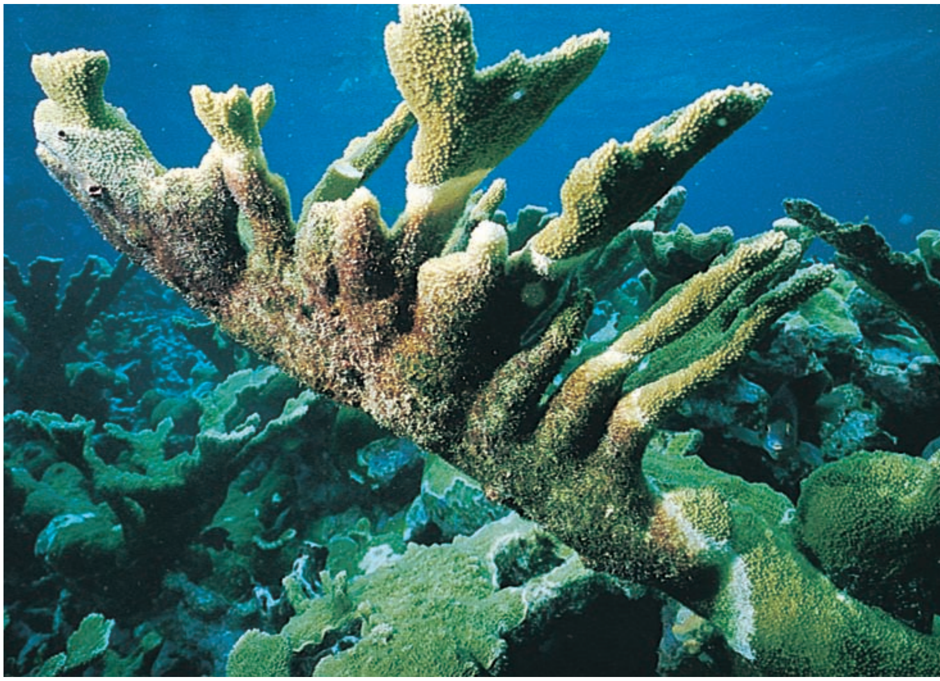


FIGURE 14.17 The elkhorn coral (*Acropora palmata*) is a dominant coral on the reef slopes of fringing reefs in the Caribbean and Florida. Its broad branches rise parallel to the surface to collect light. This colony suffers from a disease known as white-band disease (see “Coral Reefs,” p. 403).

The barrier reef consists of a **back-reef slope,** a reef flat, and a **fore-reef slope,** which corresponds to the reef slope of a fringing reef and has a reef crest. The back-reef slope may be gentle or as steep as the fore-reef slope. It is protected from waves by the rest of the reef, but waves wash large amounts of sediment from the reef down the slope. As a result, coral growth is often not as vigorous on the back-reef slope as on the fore-reef slope. This is not

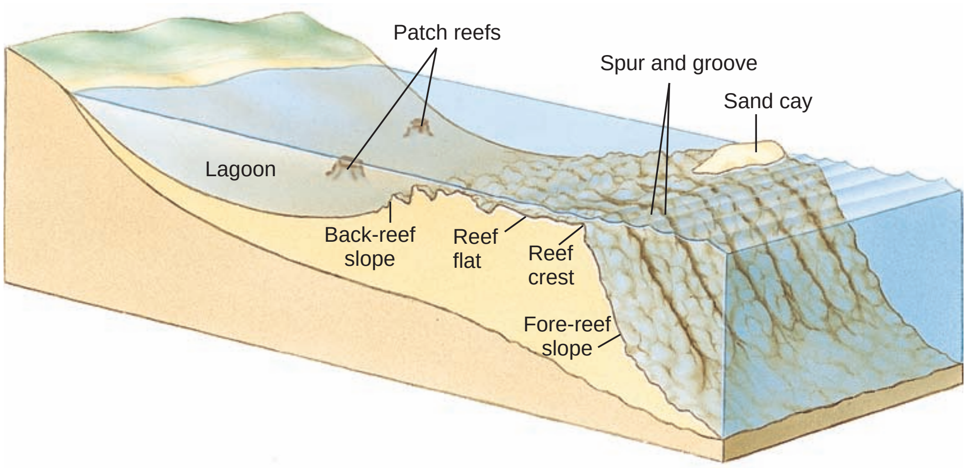


FIGURE 14.18 Typical structure of a barrier reef.

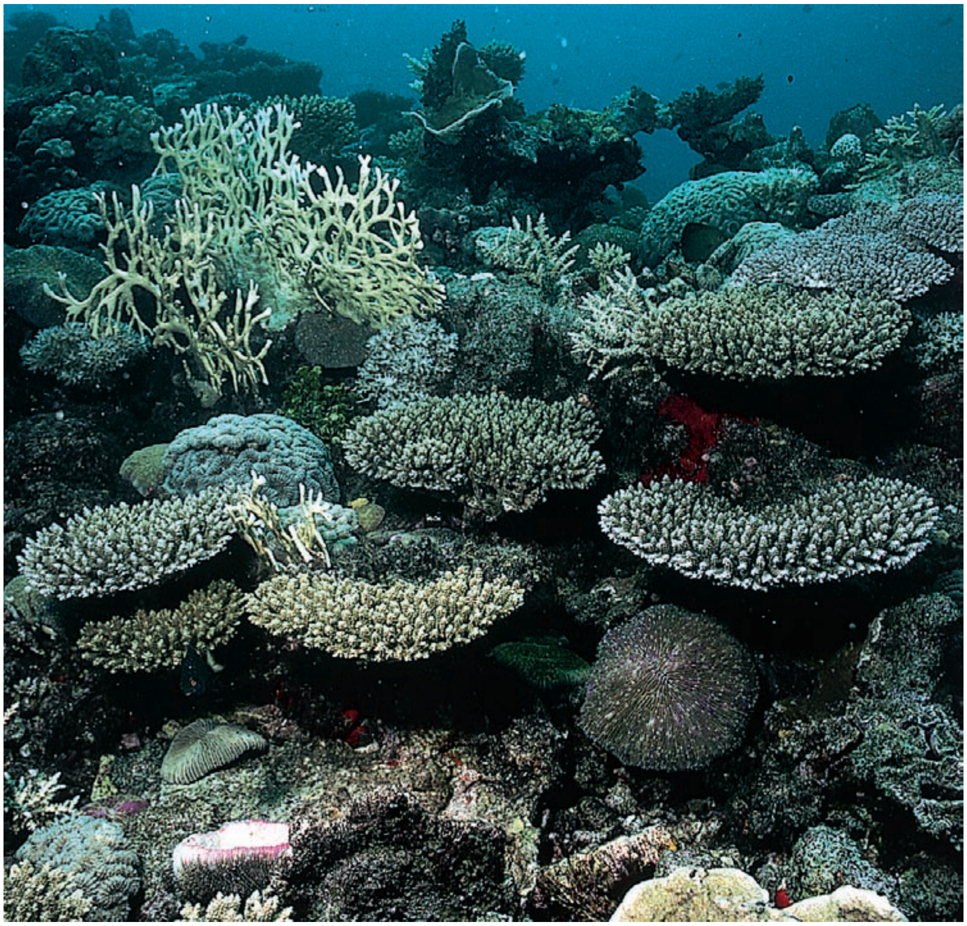


FIGURE 14.19 A rich back-reef slope on a Pacific barrier reef.

always true; some back-reef slopes, especially gentle ones, have luxuriant coral growth (Fig. 14.19).

The reef flat, like that on fringing reefs, is a shallow, nearly flat platform. Sand and coral rubble patches are interspersed with seagrass or seaweed beds, soft corals, and patches of dense coral cover. Waves and currents may pile up sand to form small sand islands called **sand cays** or, in the United States, **keys.**

The richest coral growth is usually at the outer reef crest. There may be a well-developed algal ridge if the reef is exposed to wave action, with coral growth most luxuriant just below the crest. Exposed fore-reef areas often have a series of finger-like projections alternating with sand channels (Figs. 14.18 and 14.20). There is still debate about what causes these formations, known as **spur-and-groove** formations or **buttresses.** The wind, waves, or both are definitely involved, because spur-and-groove formations develop primarily on reef slopes that are exposed to consistent strong winds. These formations are found on atolls and some fringing reefs as well as barrier reefs.

Fore-reef slopes vary from relatively gentle to nearly vertical. The steepness depends on the action of wind and waves, the amount of sediment flowing down the slope, the depth and nature of the bottom at the reef base, and other factors. As with other types of reefs, the abundance and diversity of corals on the fore-reef slope generally decrease with depth. The growth form of the corals also changes down the slope. At the crest, under the pounding of the waves, the corals are mostly stout and compact; many are massive (see Fig. 14.7). Below the crest there is great variety in form. Whether they form branches, columns, or whorls, corals in this zone often grow vertically upward. This may be an adaptation for competition. Corals that grow upward like skyscrapers rather than outward need less space to attach. They are also less likely to be shaded, and if they spread out at the top, can shade out neighboring corals and algae. Deeper on the reef slope, corals tend to grow in flat sheets, which probably helps them collect light (see Fig. 10.1).

The largest and most famous barrier reef is the Great Barrier Reef. It runs more than 2,000 km (1,200 mi) along the northeastern coast of Australia, varying in width between about 15 and 350 km (10 to 200 mi) and covering an area of over 225,000 km^2 (80,000 mi^2). Though not the longest reef in the world, it covers such a large area and is so complex and well developed that it is generally regarded as the largest reef structure. Actually, the Great Barrier Reef is not a single reef but a system of more than 2,500 smaller reefs, lagoons, channels, islands, and sand cays (Fig. 14.21).

The largest barrier reef in the Caribbean lies off the coast of Belize, Central America. Other major barrier reefs include the Florida Reef Tract and barrier reefs associated with the islands of New Caledonia, New Guinea, and Fiji in the Pacific. There are many other smaller barrier reefs, especially in the Pacific. Like the Great Barrier Reef, these usually are not single reefs but complex systems of smaller reefs.

Atolls

An atoll is a ring of reef, and often islands or sand cays, surrounding a central lagoon (Figs. 14.22 and 14.23). The vast majority of atolls occur in the **Indo-West Pacific region,** that is, the tropical Indian and western Pacific oceans. Atolls are rare in the Caribbean and the rest of the tropical Atlantic Ocean. Unlike fringing and barrier reefs, atolls can be found far from land, rising up from depths of thousands of meters or more. With practically no land around, there is no river-borne silt and very little freshwater runoff. Bathed in pure blue ocean water, atolls display spectacular coral growth and breathtaking water clarity. They are a diver's dream.

Atoll Structure Atolls range in size from small rings less than a mile across to systems well over 30 km (20 mi) in diameter. The two largest atolls are Suvadiva, in the Maldive Islands of the Indian Ocean, and Kwajalein, one of the Marshall Islands in the central Pacific. These atolls cover areas of more than 1,200 km^2 (700 mi^2). Atolls may include a dozen or more islands and be home to thousands of people.

An atoll's reef flat is much like the reef flat on a fringing or barrier reef: a flat, shallow area. The fore-reef and back-reef slopes can now be thought of as outer and inner slopes, respectively, since they extend all the way around the ring-shaped atoll.

Atoll reef crests are strongly influenced by wind and waves. Because most atolls lie in the **trade winds** belt, the wind usually comes from a consistent direction. Consequently, the wind affects various parts of the atoll in different ways. Encrusting coralline algae, which can endure the constant pounding of waves, build a distinct algal ridge on the reef crest of the **windward** side of the atoll, the side that faces the prevailing wind. On the few Caribbean atolls, coralline algae may be replaced by especially wave-resistant corals. The algal ridge is less prominent or absent on the **leeward,** or sheltered, side of the atoll. Spur-and-groove formations, too, are better developed on the windward side.

The fore-reef, or outer, slope is nearly vertical, though there is usually a series of ledges and overhangs. The rocky wall of the reef extends down to great depths, far beyond the limit of living corals themselves. The water may be hundreds, even thousands, of meters deep just a stone's throw from the reef.

The lagoon, on the other hand, is relatively shallow, usually about 60 m (195 ft) deep. The bottom of a lagoon is very uneven, with many depressions and coral pinnacles. Some pinnacles rise almost to the surface, where they may form "mini-atolls," small rings of coral within the lagoon.

Atolls are rings of reef, with steep outer slopes, that enclose a shallow lagoon.

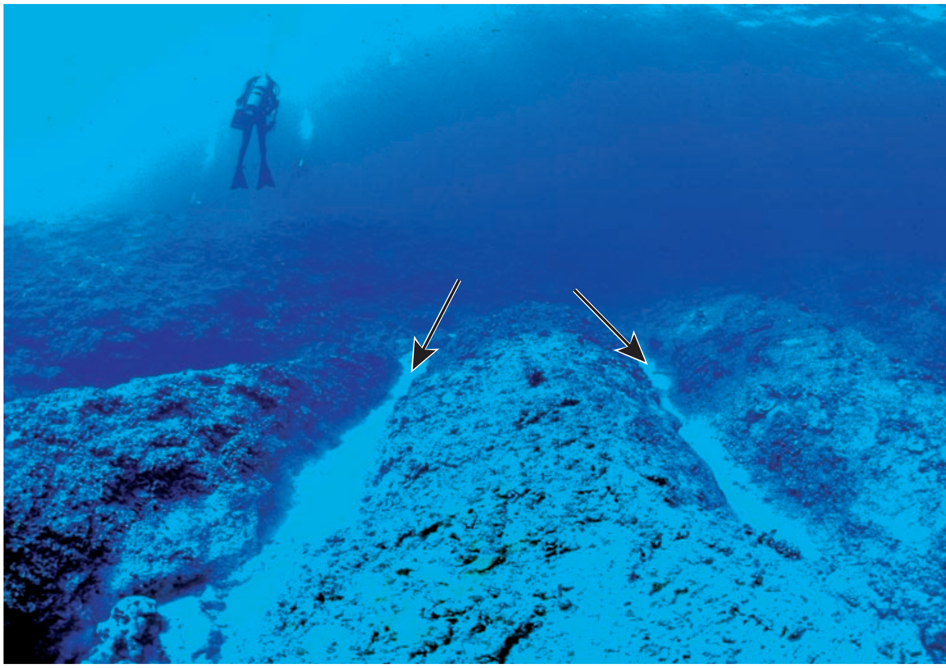


FIGURE 14.20 Spur-and-groove formations at Kure atoll in the northwestern Hawaiian Islands. The elevated ridges are the coral spurs; the light-colored grooves (arrows) channel sand down the reef slope. The northwestern Hawaiian Islands include 70% of the coral reef in United States waters and are one of the largest relatively pristine reef areas in the world.

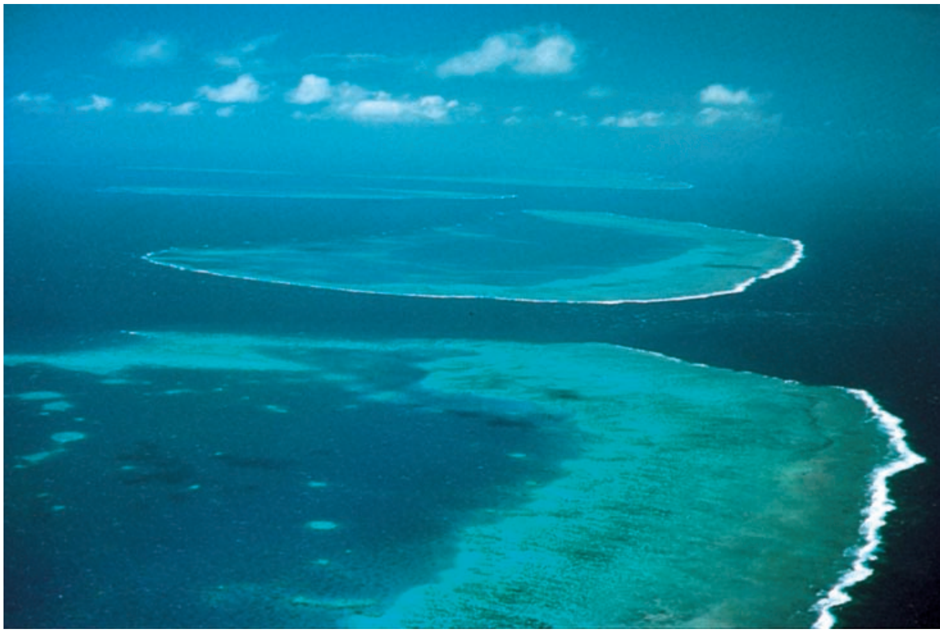


FIGURE 14.21 The Great Barrier Reef is a complicated system of thousands of small reefs, sand cays, and lagoons. Shown here are four reefs that are part of the Great Barrier Reef Marine Park. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

The trade winds, the steadiest winds on earth, blow from latitudes of about 30° toward the Equator.
- Chapter 3, p. 49; Figure 3.18

Subsidence The slow sinking into the *mantle* of a part of the earth's crust that contains a landmass.
- Chapter 11, p. 242

How Atolls Form When atolls were discovered, scientists were at a loss to explain them. It was known that corals can grow only in shallow water, yet atolls grow right in the middle of the ocean, out of very deep water. Therefore, the atoll could not have grown up from the ocean floor. If the reefs grew on some kind of shallow structure that was already there, like a seamount, why is there no sign of it? The islands on atolls are simple sand cays that have been built by the accumulation of reef sediments and would not exist without the reef. They are *products* of the reef and could not provide the original foundation for reef growth. Finally, why do atolls always form rings?

The puzzle of atoll formation was solved by Charles Darwin in the mid-nineteenth century. Darwin is most famous, of course, for proposing the theory of evolution by natural selection, but his theory of atoll formation was another important contribution to science.

Darwin reasoned that atolls could be explained by reef growth on a subsiding island. The atoll gets its start when a deep-sea volcano erupts to build a volcanic island. Corals soon colonize the shores of the new island, and a fringing reef develops (Fig. 14.24*a*). As with most fringing reefs, coral growth is most vigorous at the

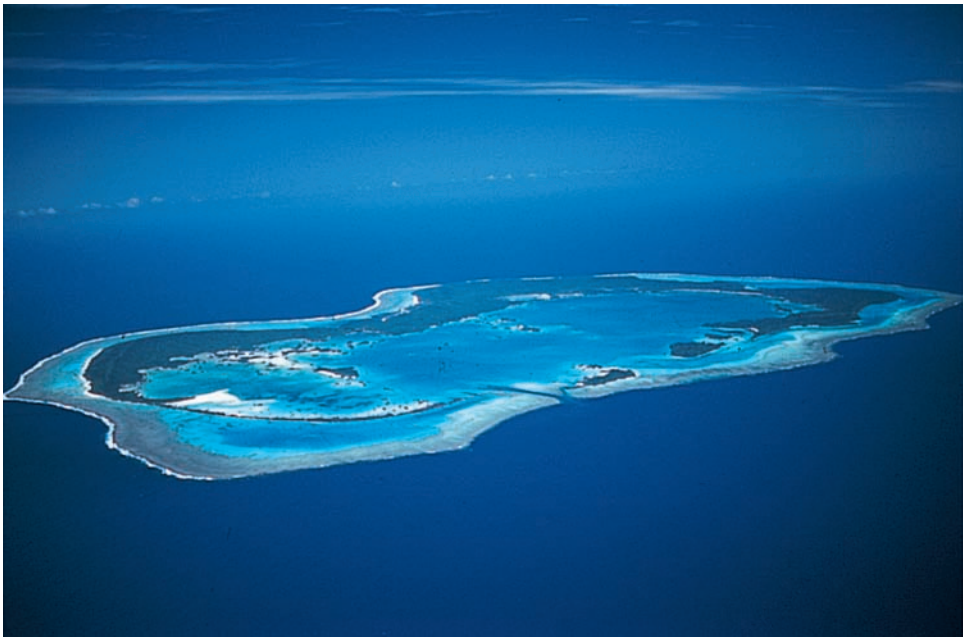


FIGURE 14.22 Fulanga atoll, in the South Pacific nation of Fiji.

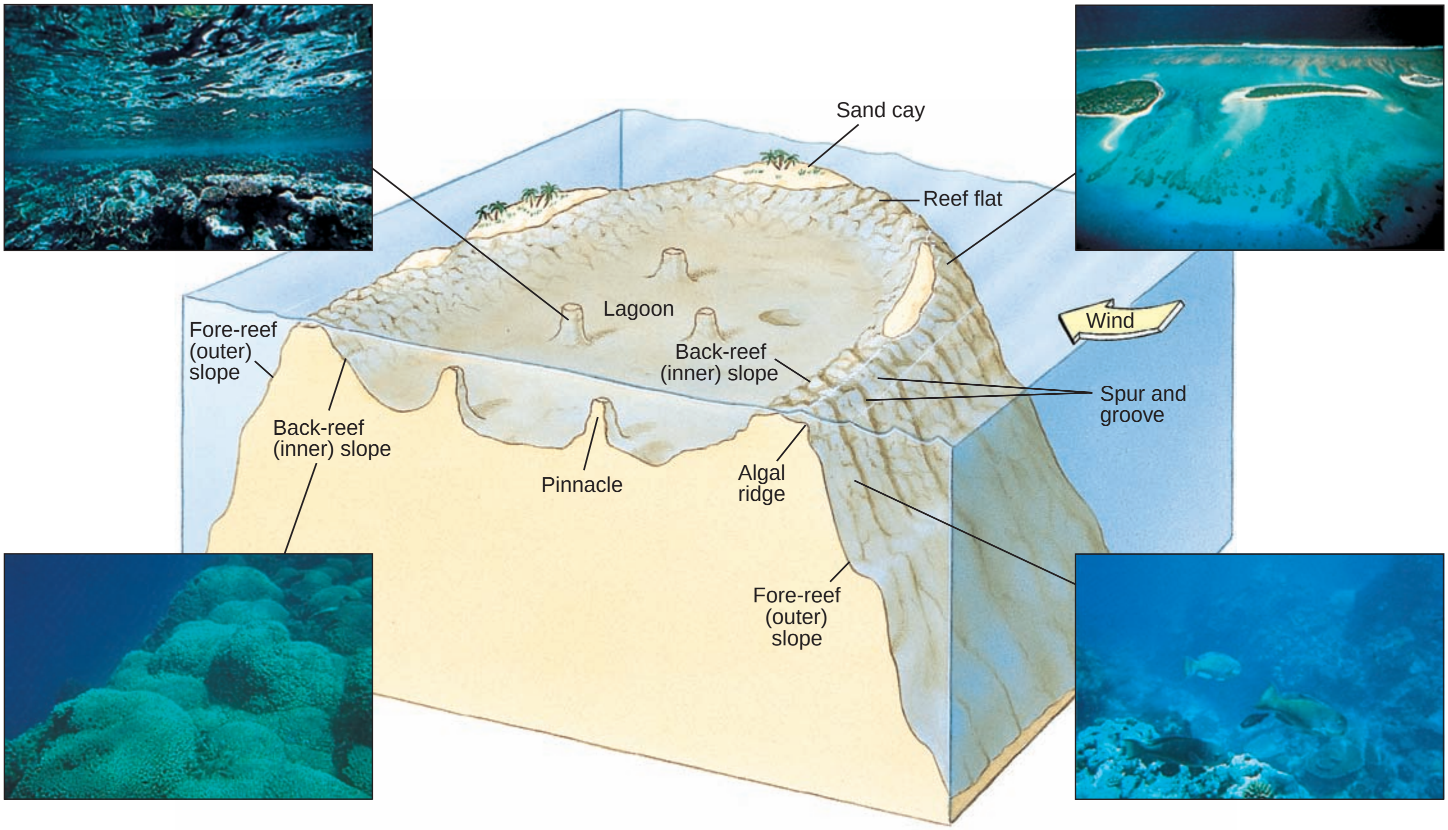


FIGURE 14.23 Typical structure of an atoll.

Deep-Water Coral Communities

Tropical coral reefs bask in the sunlight of shallow water, but more than 700 species of corals live in the cold and darkness of deep water. Deep-water corals occur in all the world's oceans to depths of over 6,000 m (20,000 ft). They do not harbor zooxanthellae, which in the absence of sunlight would be of no use to the host coral. They feed by capturing zooplankton with their tentacles, and generally grow where there are strong currents to bring in food.

About 20 deep-water coral species build or contribute to large mounds on the sea floor known as bioherms. The mounds are usually found on the continental slope or on seamounts and other underwater features at depths of up to 1,500 m (5,000 ft). In some places, Norwegian fjords for example, they occur in water as shallow as 40 m (130 ft). These structures are often called "coral reefs," but the term "reefs" was originally a nautical term for areas of hard bottom shallow enough for ships to run aground, and the geological definition of coral reefs refers to a solid calcium carbonate structure built by corals. Although deep-water coral mounds contain large amounts of calcareous coral fragments, they are mostly mud. The mounds also appear to be a product of circulation patterns that favor the passive accumulation of sediment and coral fragments, rather than structures actively built by the corals. Scientists have also speculated that the mounds might form around cold seeps and rely in part on chemosynthesis.

The largest known deep-water coral mounds, dominated by the branching coral *Lophelia pertusa,* are in the northeastern Atlantic off the coast of Britain and Scandinavia. Individual mounds grow more than 300 m (1,000 ft) above the surrounding muddy bottom, with a base more than 5 km (3 mi) in diameter. Mound complexes can extend for as far as 45 km (30 mi).

Whether you call them coral reefs or not, *Lophelia* mounds support rich and diverse communities. The coral branches and broken fragments provide shelter and a hard surface where other sessile species can attach. Relatively few fishes, about 25 species, are known to associate with *Lophelia* mounds, but so far biologists have found more than 1,300 invertebrate species. There could well be more. The *Lophelia* mounds in the northeastern Atlantic have been known since the nineteenth century but have only really been studied in the last two decades when advances in deep-sea exploration technology revealed their true extent and diversity. Mounds made by *Lophelia* and other deep-water corals occur in many other parts of the ocean, and new mounds are regularly discovered as deep-sea exploration continues.

Like seamount communities (see "Biodiversity in the Deep Sea," p. 375), deep-water coral communities on the continental slope are increasingly threatened by trawl fishing. As shallow-water fisheries are depleted, trawlers are forced into ever-deeper water. The trawls shatter the fragile corals and dig great gouges in the sea bed. Some countries have prohibited trawling in areas of known coral mounds, but many of these diverse communities remain unprotected.

Intact *Lophelia pertusa* mounds are home to many fishes and invertebrates.

Trawl damage to a *Lophelia* mound.

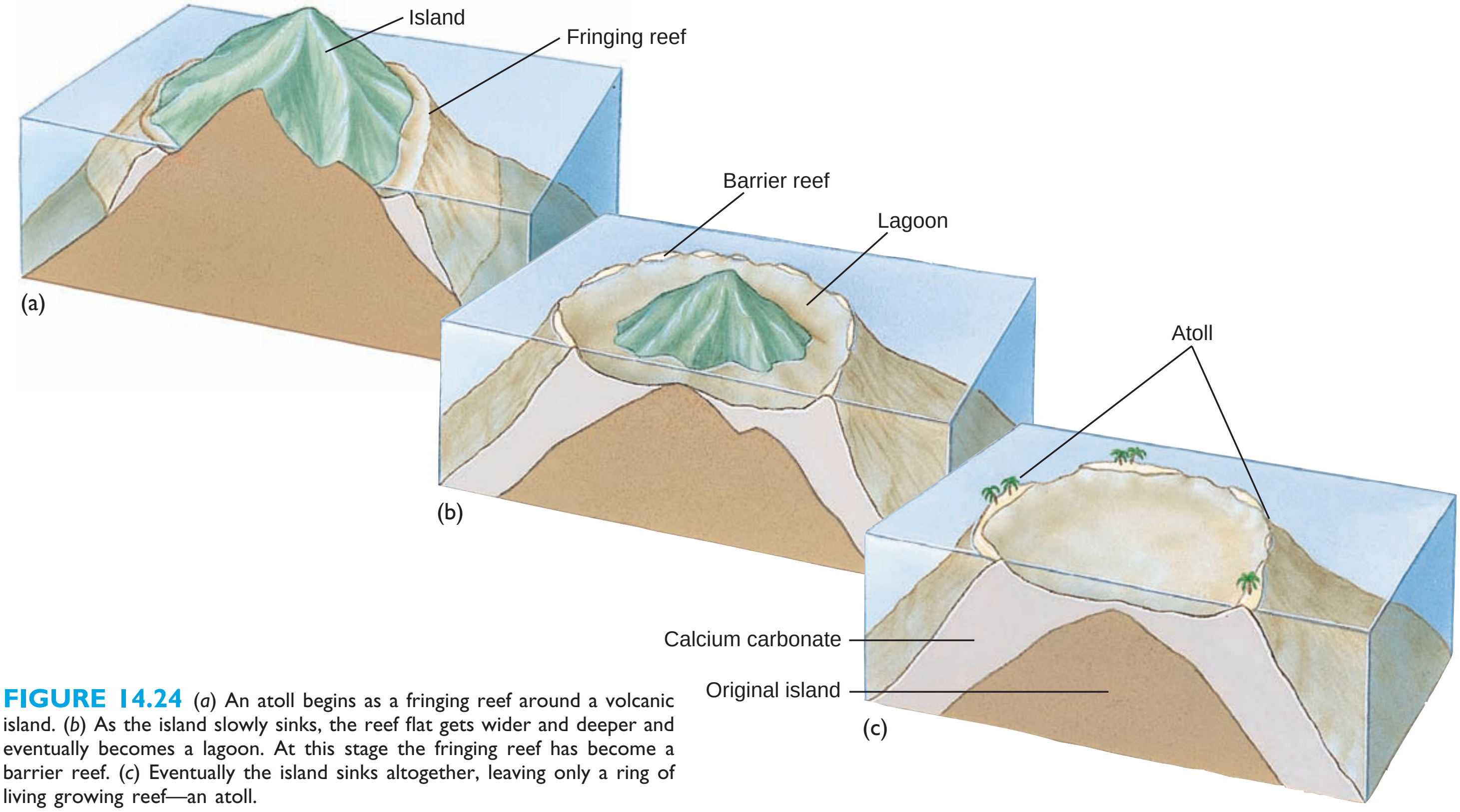


FIGURE 14.24 (*a*) An atoll begins as a fringing reef around a volcanic island. (*b*) As the island slowly sinks, the reef flat gets wider and deeper and eventually becomes a lagoon. At this stage the fringing reef has become a barrier reef. (*c*) Eventually the island sinks altogether, leaving only a ring of living growing reef—an atoll.

outer edge of the reef. The inner reef is strongly affected by sediment and runoff from the island.

Surprisingly, Darwin's explanation of atoll formation was pretty much ignored for a century while scientists proposed various other hypotheses, none of which held up. Finally, scientists found conclusive evidence that Darwin was right. Unlike other hypotheses for atoll formation, Darwin's hypothesis predicted that, below the thick calcium carbonate cap formed by the reef, there should be volcanic rock—the original island. In the 1950s the United States Geological Survey drilled several deep holes on Enewetak atoll in the Marshall Islands. These cores revealed exactly what Darwin predicted: volcanic rock far beneath the calcium carbonate of the reef. The thickness of the carbonate cap is impressive: The volcanic island underlying Enewetak is covered by more than 1,400 m (4,600 ft) of calcium carbonate!

There are, of course, a few details to be added to the picture, in particular the effects of changes in sea level (see "Climate and Changes in Sea Level," p. 33). When sea level is low, atolls may be left above the surface. The corals die and the reef is eroded by the wind and rain. If sea level rises rapidly, the atoll may be drowned, unable to grow in deep water. In either case, corals recolonize the atoll when the sea level returns to "normal."

THE ECOLOGY OF CORAL REEFS

Coral reefs may be impressive to geologists, but to the biologist they are simply awesome. They are easily the richest and most complex of all marine ecosystems. Literally thousands of species may live on a reef. How do all these different species live? How do they affect each other? What is their role in the reef ecosystem? These and countless other questions fascinate coral reef biologists.

Our ability to answer the questions, however, is surprisingly limited. This is partly because reefs are so complicated. Just keeping track of all the different organisms is hard enough; the task of figuring out what they all *do* is mind-boggling. Furthermore, until the last half century or so most marine biologists lived and worked in the temperate regions of the Northern Hemisphere, far from the nearest reef. As a result, relatively few biologists studied reefs. Tremendous progress has been made in recent years, but there is still much to learn. The rest of this chapter summarizes what is known about the ecology of coral reefs and points out some of the important questions that remain.

The Trophic Structure of Coral Reefs

The tropical waters where coral reefs are found are usually poor in nutrients and therefore have very little phytoplankton or **primary production.** In these barren waters, coral reefs are oases of abundant life. How can such rich communities grow when the surrounding sea is so unproductive?

A good part of the answer lies in the mutualistic relationship between corals and their zooxanthellae. We have already learned what the zooxanthellae do for the coral: They provide food and help make the calcium carbonate skeleton. In return the zooxanthellae get not only a protected place to live, but also a steady supply of carbon dioxide and nutrients such as **nitrogen** and **phosphorus.** Most of the coral's nitrogen and phosphorus waste products are not released into the water. Instead, they are taken up and used as nutrients by the zooxanthellae. Using sunlight, the zooxanthellae incorporate the nutrients into organic compounds, which are passed on to the coral. When the coral breaks down the organic matter, the nutrients are released and the whole process begins again (see Fig. 14.8). The nutrients are recycled, so that far fewer nutrients are needed than would otherwise be the case.

Nutrient recycling occurs not just between corals and their zooxanthellae, but among all the members of the coral reef community. Sponges, sea squirts, giant clams, and other reef invertebrates have symbiotic algae or bacteria and recycle nutrients just as corals do. Recycling also takes place outside the bodies of reef organisms. When fishes graze on seaweeds, for example, they excrete nitrogen, phosphorus, and other nutrients as waste. These nutrients are quickly taken up by other algae. Many corals provide shelter to schools of small fish (see Fig. 8.20). The fish leave the coral at night to feed and return during the day. The waste products of the fish can be an important source of nutrients and help the coral grow faster. In this way nutrients are cycled from the fish's prey to the fish to the coral. Nutrients pass through the community again and again in this cycle of feeding and excretion.

Coral reef communities use nutrients very efficiently as a result of recycling. The recycling is not perfect, however, and some nutrients are lost, carried away by the currents. Thus, the reef still needs a supply of new nutrients. Recycling alone is not enough to account for the high productivity of reefs.

The reef is able to provide some of its own nutrients. Coral reefs have among the highest rates of **nitrogen fixation** of any natural community. The main nitrogen fixers are cyanobacteria, especially a free-living one called *Calothrix* and another group that lives symbiotically in sponges. There is evidence that corals, too, have symbionts that fix nitrogen, providing nutrients for the zooxanthellae. Just what the symbionts are is not known. Because of this nitrogen fixation, nitrogen probably does not limit most coral reef communities, though not all reef biologists agree about this.

Ocean currents bring in additional nitrogen and, more importantly, phosphorus and other nutrients that are not produced on the reef. Corals, bacteria, algae, and other organisms absorb nutrients directly from the water. Even though the water is nutrient-poor, if enough water washes over the reef the nutrients add up. In business terms, this is a low-margin, high-volume proposition. More importantly, the water carries zooplankton, a rich nutrient source. When zooplankton are captured by the "wall of mouths," the nutrients in the zooplankton are passed on to the reef community. In fact, many biologists think that corals eat zooplankton to get nutrients for their zooxanthellae as much as to feed themselves. Animals like seabirds, dolphins, and large fishes that spend part of their time around reefs but venture out into the open ocean to feed also transfer nutrients from oceanic waters to the reef community.

Coral reefs are very productive even though the surrounding ocean water lacks nutrients because nutrients are recycled extensively, nitrogen is fixed on the reef, and the zooplankton and nutrients that occur in the water are used efficiently.

The production and efficient use of nutrients by coral reef communities result in high primary productivity. This is reflected in the overall richness of the community. Scientists aren't sure, however, just how much primary production there is on coral reefs, or which particular organisms are the most important producers. There is no doubt that zooxanthellae are very important, but because they live inside corals, it is hard to measure exactly how much organic matter they produce. For a time it was thought that very few animals eat coral, since there is so little live tissue on a coral colony. It was therefore believed that, even though zooxanthellae produce a lot of organic matter, most of it is consumed by the coral and not much passed on to the rest of the community. As biologists looked closer, however, they found more and more animals that eat corals or their products (Fig. 14.25). Primary production by coral zooxanthellae therefore may be important not only to corals but to the community at large. Exactly how much production corals and their zooxanthellae contribute is still unknown.

Primary Production The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs, that is, the production of food.

- Chapter 4, p. 68

Nitrogen Fixation The conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.

- Chapter 5, p. 93; Table 5.1

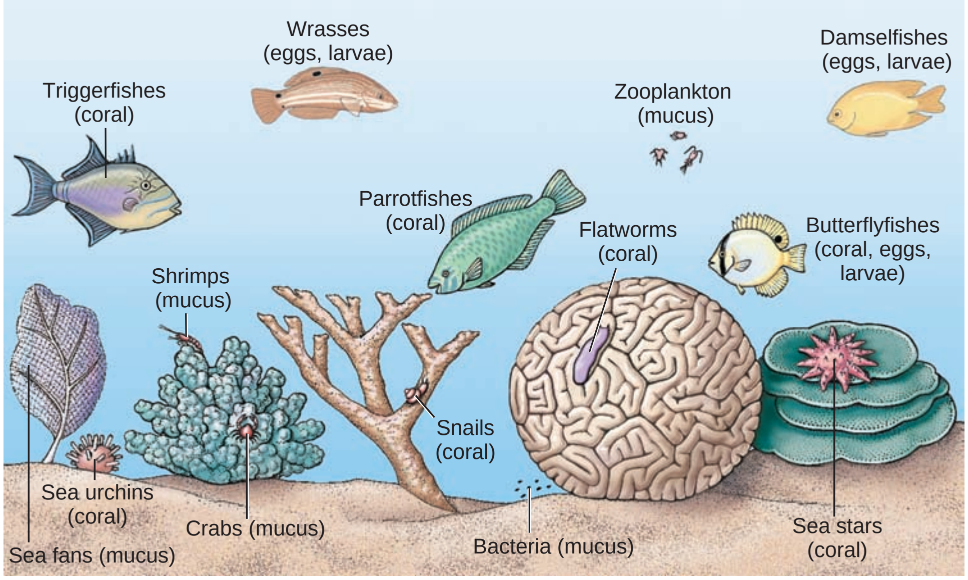


FIGURE 14.25 A number of animals eat coral directly, and many others feed on the mucus that corals produce or on coral eggs and larvae. The primary production of coral zooxanthellae is thus passed on to coral feeders, and then to the animals that eat them.

Seaweeds are also important primary producers on the reef (Fig. 14.26), especially the small, fleshy or filamentous types that are called **turf algae** because they often grow in a short, thick turf on the reef flat. A great many fishes, sea urchins, snails, and other animals graze on these seaweeds. The turf algae may perform more photosynthesis on the reef than the zooxanthellae, but biologists are not sure.

Zooxanthellae and turf algae are probably the most important primary producers on coral reefs.

Cyanobacteria and coralline algae are also primary producers on coral reefs. They probably account for less primary production than do zooxanthellae and turf algae.

Coral Reef Communities

With so many species on coral reefs, the interactions among them are exceedingly complex. What is known about these interactions is fascinating; what remains to be learned will be even more so.

Competition Space is at a premium on coral reefs, as it is in the rocky intertidal (see "The Battle for Space," p. 248). Corals, seaweeds, and many others need to attach to a hard surface. Corals and seaweeds need not just space but space in the sunlight. The reef is crowded, and most of the available space is taken. As a result the sessile organisms, those that stay in one place, must compete for space.

Sessile coral reef organisms must compete for space. Corals and seaweeds compete for light as well.

Corals compete for space in different ways. The fast-growing ones tend to grow upward and then branch out, cutting their neighbors off from the light. Other corals take a more direct approach and actually attack their neighbors (Fig. 14.27). Some use their mesenterial filaments for this. When they contact another coral, they extrude the filaments and digest away the tissue of the other coral. Still other corals develop special long tentacles called **sweeper tentacles** that are loaded with nematocysts and sting neighboring colonies. Corals differ in their aggressive abilities. The most aggressive corals tend to be slow-growing, massive types, whereas the less aggressive forms are usually fast-growing, upright, and branching. Both strategies have their advantages, and both kinds of corals thrive on the reef.

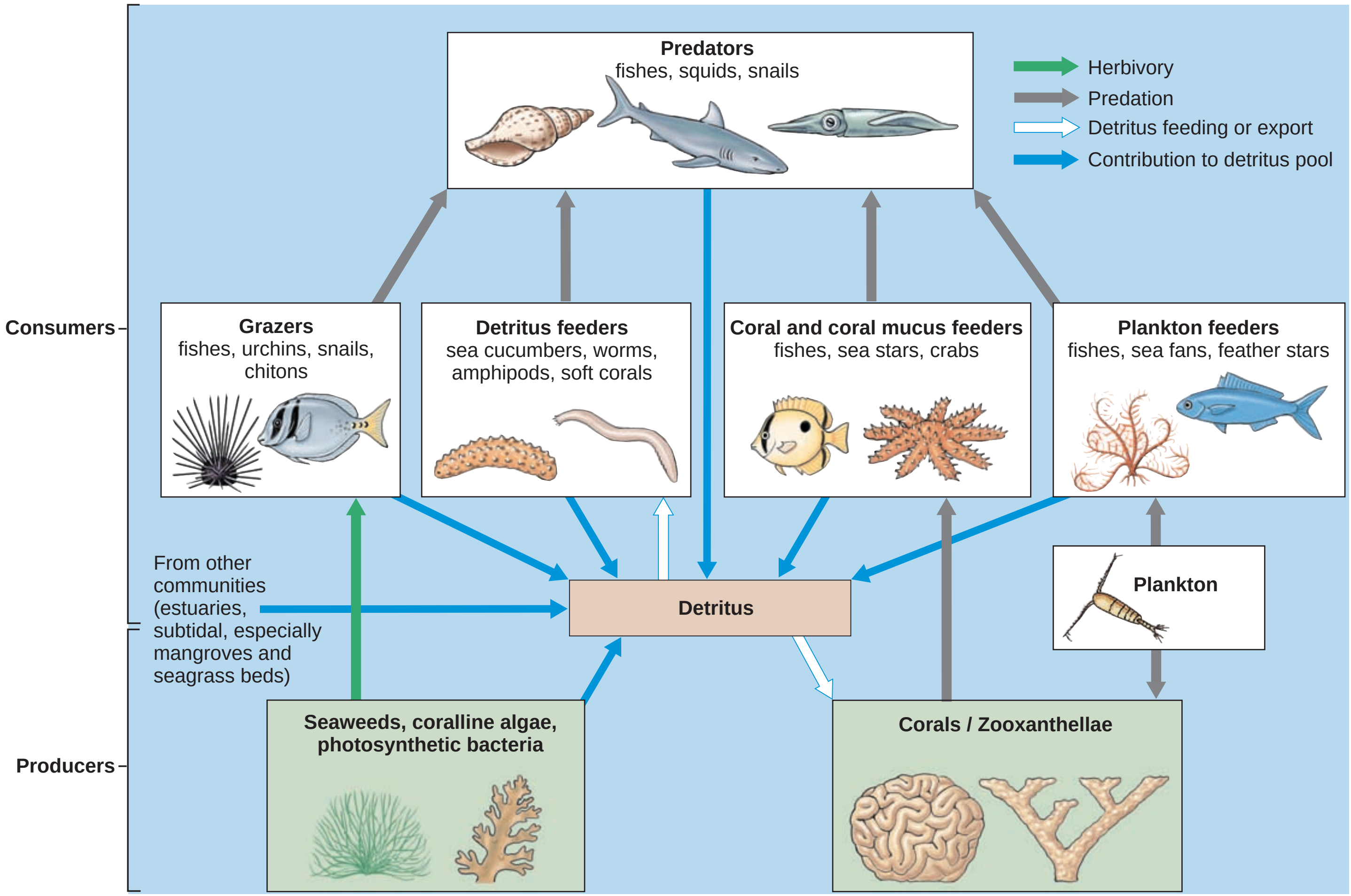

Predators
fishes, squids, snails
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool
Consumers
Grazers
fishes, urchins, snails, chitons
Detritus feeders
sea cucumbers, worms, amphipods, soft corals
Coral and coral mucus feeders
fishes, sea stars, crabs
Plankton feeders
fishes, sea fans, feather stars
From other communities (estuaries, subtidal, especially mangroves and seagrass beds)
Detritus
Plankton
Producers
Seaweeds, coralline algae, photosynthetic bacteria
Corals / Zooxanthellae

FIGURE 14.26 A generalized coral reef food web. Coral reefs are extremely diverse, and most components include many organisms in addition to those listed here.

EYE ON SCIENCE

Reef Check

So you want to try your hand at marine biology? Have we got a deal for you! For the last two decades or so scientists have been increasingly concerned about the future of the world's coral reefs. But there are tens of thousands of reefs scattered around the world, often in remote locations. There are only so many reef biologists, like most scientists chronically short of research funding. How can a limited number of scientists, with limited resources, monitor the global status of coral reefs?

Since 1996 the Reef Check program has provided part of the answer by enlisting the services of an enthusiastic volunteer "army." Every year millions of recreational divers journey to the world's coral reefs—the more remote the better—to explore and experience their wonders. Most divers are keenly interested in marine life, know quite a bit about it, and want to help protect it. Best of all (from a cash-strapped scientist's point of view), they pay for their own travel, food, and lodging, and even bring their own equipment!

To take advantage of this untapped resource, Reef Check designed methods that are simple enough to be used by people with no formal scientific background but still produce reliable, scientifically valuable information for assessing the condition of reefs. After a short training session, Reef Check teams don their dive gear to survey a site. After recording a basic description of the site on the basis of a predefined set of questions, they stretch a measuring tape at a given depth along the bottom. Then they record the type of bottom (live coral, dead coral, algae, etc.) at specified points under the tape and count designated "indicator" organisms. The indicator organisms are selected to be easy to identify and distinguish from other species by sight, without professional training, and to be a good index of some aspect of human impact on the reef. Spiny lobsters and groupers, for example, are a good indicator of fishing pressure because these tasty critters are usually among the first targets of fishers.

Reef Check provided the first-ever global snapshot of the state of coral reefs, confirming their widespread degradation, and Reef Check surveys since have confirmed that probably no reefs have entirely escaped human impacts. But the work has also shown that, given wise use and management, reefs are able to recover. In addition to its regular surveys Reef Check now helps support improvements in the management and protection of reefs and recently extended its approach to rocky subtidal reefs along the California coast. So if you're a diver looking for a holiday that's a little different and would like to get a taste of being a marine biologist while helping protect coral reefs and having a lot of fun in the process, check out ReefCheck.org.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

The two main ways in which corals compete for space are by overgrowing their neighbors and by directly attacking them.

Corals compete for space and light not only with each other, but also with seaweeds and sessile invertebrates. Like corals, encrusting algae have to produce a calcium carbonate skeleton and therefore grow relatively slowly. They tend to be found in places where corals don't do well because of sedimentation, wave action, or predation.

Under the right conditions seaweeds, except for encrusting forms, can grow much faster than either corals or encrusting algae. Even with the nitrogen fixation and nutrient cycling that occur on reefs, seaweeds are probably somewhat nutrient-limited most of the time. Hence, they grow fairly slowly. The reef also has an abundance of hungry grazers that eat the seaweeds. The combination of nutrient limitation and grazing keeps the seaweeds in check. If the nutrient levels increase or the grazers are removed, seaweeds may rapidly take over, overgrowing and choking out corals and other organisms.

Soft corals are also important competitors for space on reefs (Fig. 14.28), and in some places they make up almost half the living tissue. Like most seaweeds, soft corals lack a calcium carbonate skeleton and are able to grow faster than hard corals. Some soft corals contain sharp little calcium carbonate needles, or **sclerites,** that discourage predation. Many of them also contain chemicals that are toxic or taste bad to predators. Because of these defense mechanisms, only a few specialized predators eat soft corals. The defensive chemicals can also be released into the water, where they kill hard corals that come too close (Fig. 14.27). Another competitive advantage enjoyed by some soft corals is that they are not completely sessile. Though they stay in one place most of the time, they can move about slowly. This helps them invade and occupy available space on the reef.

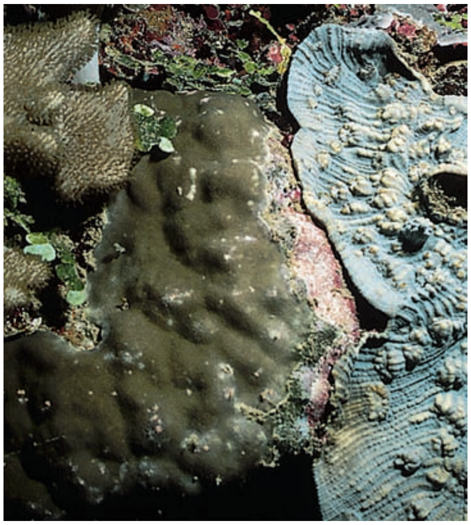


FIGURE 14.27 When different species of coral come in contact, they attack each other. The pink band separating the brown (*Porites lutea*) and blue (*Mycedium elephantotus*) corals is a dead zone where the blue coral has killed the brown one in the process of overgrowing it. The width of the pink band corresponds to the length of the blue coral's tentacles. To the upper left of the brown coral is a soft coral (*Sarcophyton*), which may be attacking the brown coral by releasing poison. The brown coral seems to be stuck between a rock and a soft place!

Soft corals are important competitors for space on reefs. They grow rapidly, are resistant to predators, and can occasionally move about.

With all these competitive weapons at their disposal, why don't soft corals take over? Not much is known about how soft corals compete with reef-building corals and other reef organisms or what determines the winner. Many soft corals appear to have shorter lives than reef-building corals, although some may live for decades. They are also more easily torn away by storm waves. They have symbiotic zooxanthellae like reef-building corals but are much less efficient photosynthesizers. They also seem to depend on favorable physical conditions. It is not known how these factors interact to determine when and where soft corals successfully compete for space on the reef.

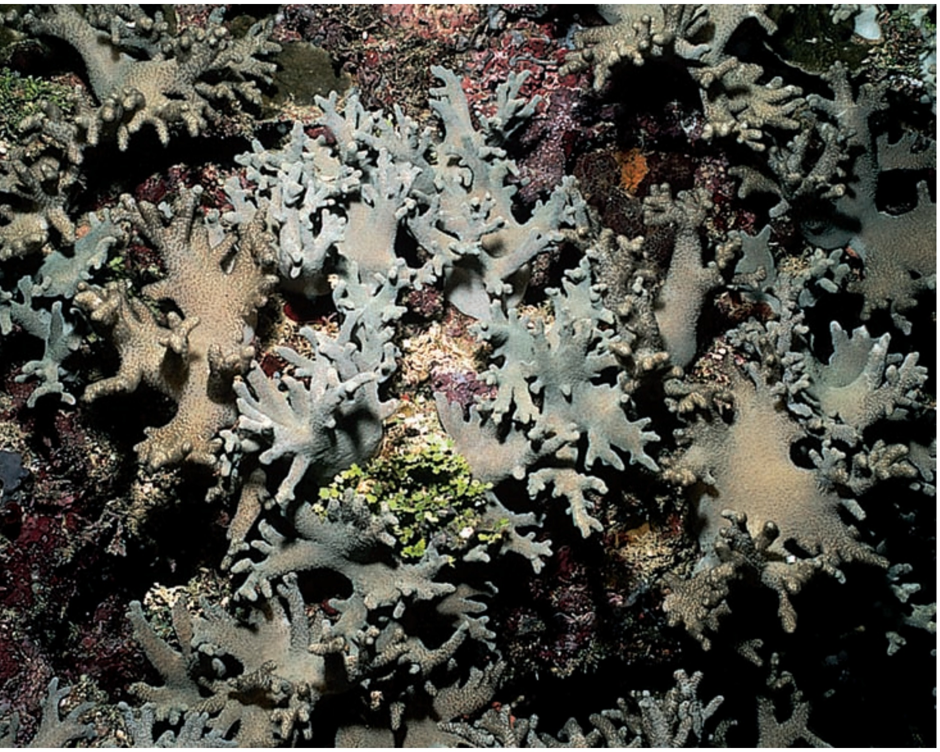


FIGURE 14.28 Soft corals can form dense patches on coral reefs, as on this reef in Papua New Guinea.

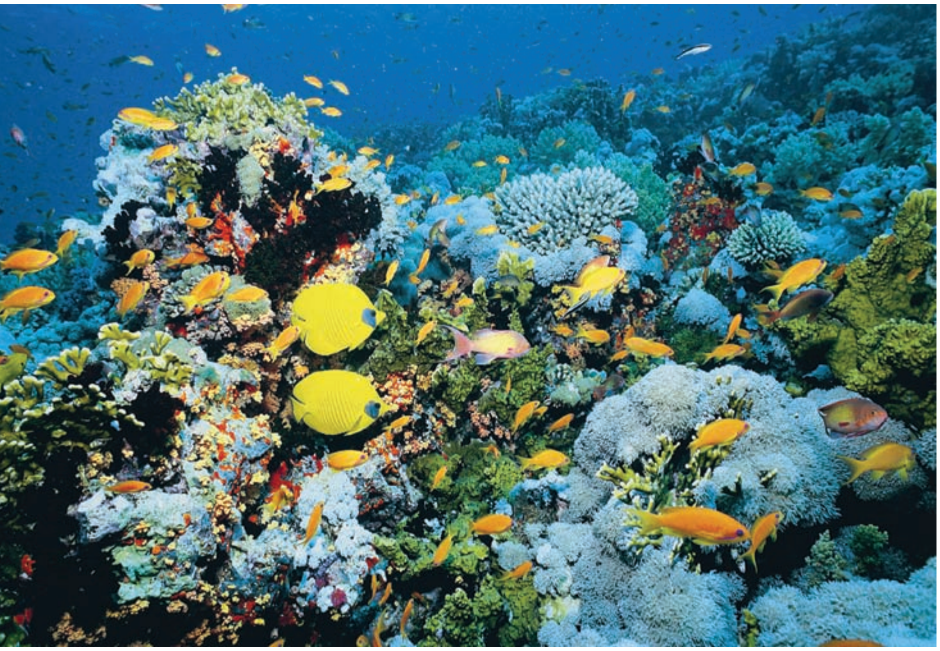


FIGURE 14.29 Diving on a coral reef is like taking a swim in a tropical fish aquarium—brightly colored fishes seem to be everywhere. The competitive relationships among the various species of fishes are poorly understood.

Like soft corals, sponges often have needle-like structures, spicules, and nasty chemicals that protect them from predators. They can be important users of space on reefs, much more so in the Caribbean than in the Pacific and Indian oceans. Part of the reason for this seems to be that there are fewer species of coral in the Caribbean than in the Indo-West Pacific. This is a result of geological history. During the most recent series of ice ages, the sea surface was cooler. Corals survived in the heart of the Indo-West Pacific region, around Indonesia and New Guinea, but many species became extinct in other parts of the ocean. When the ice age ended, corals spread out again across the Pacific, recolonizing areas where they had died out. The Caribbean, however, was not recolonized because the Isthmus of Panamá blocked their dispersal. It is thought that the Caribbean contains only those coral species that managed to survive the ice ages there.

Coral reef fishes are another group in which competition may be important. Along with corals, fishes are probably the most conspicuous and abundant animals on the reef (Fig. 14.29). Many of these fishes share similar diets; for example, many species eat coral, many graze on algae, and many are carnivores. Different species of fishes of the same feeding type at least potentially compete with each other.

There is much debate about how competition affects coral reef fishes. One hypothesis is that competition is relatively unimportant, and that the abundances of individual species are determined mainly by how many of their larvae settle out from the plankton. With favorable currents and other conditions, many larvae will be available to settle out and the species becomes abundant. If the supply of larvae is low, for example if currents carry larvae away from the reef, the species becomes rare. This is called a **pre-settlement** hypothesis because it holds that the nature of reef fish communities is determined by the availability of different species' larvae before the larvae settle.

An alternative, **post-settlement,** hypothesis is that most species have plenty of available larvae. The species that survive and become abundant are those that compete successfully for space, food, and other resources after the larvae settle, that is, as juveniles and adults. This hypothesis holds that so many different fish species can live on the reef because each does something a little different from other species, thereby avoiding competition and the risk of **competitive exclusion.** In other words, each species has its own particular **ecological niche.** According to this view, the structure of the fish community on a reef is determined by the range of resources available on that reef, and the fish communities of reefs vary because different reefs offer different resources.

It is still not clear whether the supply of larvae for settlement or post-settlement competition is more important in structuring reef fish communities. Their relative importance probably varies from species to species and from reef to reef, and other factors such as predation and natural disturbances are also important.

There are two competing schools of thought about what controls the structure of reef fish communities. One holds that reef fish abundances are determined by how many larvae are available to settle out from the plankton. The other asserts that there is an ample supply of larvae for most species, and that reef fish communities are structured by competition among juveniles and adults after the larvae settle out.

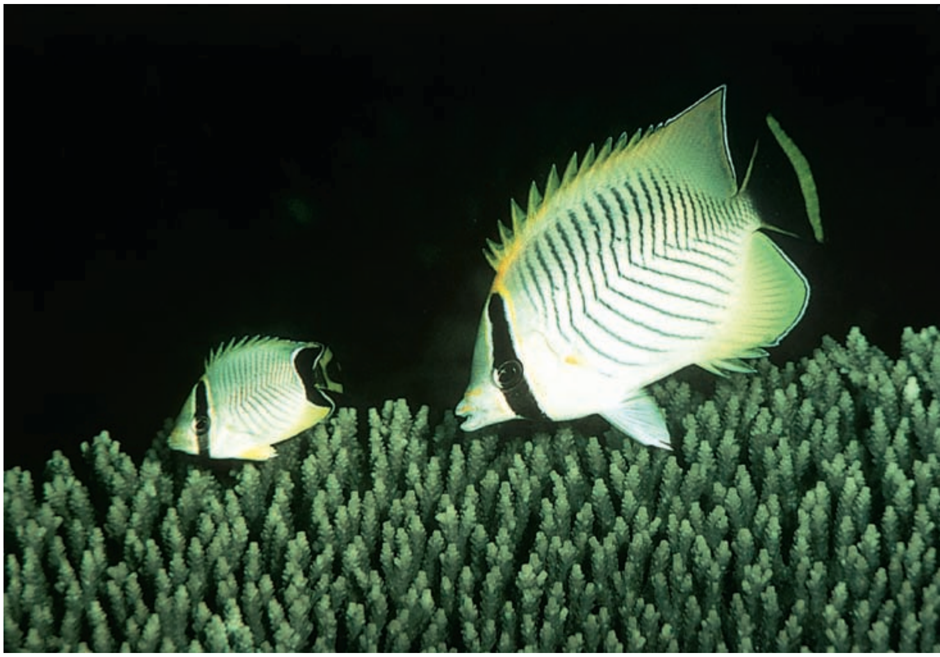


FIGURE 14.30 The chevron butterflyfish (*Chaetodon trifascialis*) is one of many reef animals that feed on corals without killing the entire coral colony. Its mouth is adapted for nipping off individual coral polyps (also see Fig. 8.28).

Predation on Corals As in other communities, predation and grazing are important in structuring coral reef communities. A variety of animals eat corals, but instead of killing the coral and eating it entirely, most coral predators eat individual polyps or bite off pieces here and there (Fig. 14.30). The coral colony as a whole survives and can grow back the portion that was eaten. In this respect, coral predation is similar to grazing by herbivores.

Coral predation affects both the number and type of corals that live on a reef, as well as how fast the reef as a whole grows. In Kāne'ohe Bay, for example, a butterflyfish (*Chaetodon unimaculatus*) slows the growth of a particular coral (*Montipora verrucosa*) that it likes to eat. When the coral is protected from the fish by a cage, it grows much faster. If it were not for the fish, this fast-growing coral would probably dominate other corals in the bay. Coral-eating snails (*Coralliophila, Drupella*) have similar effects on some reefs.

The Crown-of-Thorns Sea Star Another example of the effect of coral predators is the **crown-of-thorns sea star** (*Acanthaster planci;* Fig. 14.31). The crown-of-thorns feeds by pushing its stomach out through the mouth, covering all or part of the coral colony with the stomach, and digesting away the live coral tissue. The crown-of-thorns has distinct preferences for certain types of coral and avoids others—some corals must taste bad. Other corals harbor symbiotic crabs (see the photo on p. 115), shrimps, and fishes that discourage the sea stars by pinching and biting their **tube feet.**

The crown-of-thorns has had a major impact on some reefs. Beginning in the late 1950s, people began to notice large numbers, sometimes thousands, of the sea star on reefs scattered across the Pacific (Fig. 14.32). The sea stars in these large aggregations move en masse across the reef, consuming almost every coral in their path. Reefs recover in 10 to 15 years, though it may take longer for slow-growing coral species to grow back.

The first response to the problem was panic. Coral reefs are valuable resources: They support fisheries, tourism, and recreation and protect coastlines from tsunamis, storms, and erosion. With the crown-of-thorns apparently threatening reefs, people decided to take action and control the sea star. The first attempt backfired. With limited knowledge of the animal's biology, some people cut the sea stars into pieces and dumped them back in the sea. Because sea stars can regenerate, the pieces grew into new sea stars! More sophisticated methods, such as poisoning the sea stars, were tried, but these methods were time consuming and expensive, did not work that well, and sometimes did more harm than good. Fortunately, the outbreaks mysteriously went away by themselves. Did the sea stars starve? Did they move away? No one knows. Crown-of-thorns outbreaks are still appearing, and disappearing, without explanation.

The debate over what causes these outbreaks has been controversial and sometimes emotional. At first it seemed obvious that the outbreaks must be unnatural, with humans to blame. After all, the plagues had never occurred before. Or had they? People had only begun using scuba a short time before the sea star plagues were noticed. Even if the plagues had been occurring for a long time, there were no scientists around to see them. Geologists found fossil evidence of crown-of-thorns outbreaks

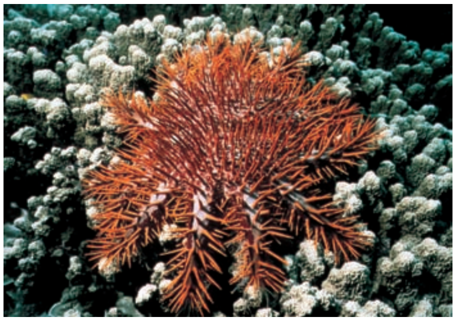


FIGURE 14.31 The crown-of-thorns sea star (*Acanthaster planci*) is an important and controversial coral predator.

Competitive Exclusion The elimination of one species by another as a result of competition.
- Chapter 10, p. 214

Ecological Niche The combination of what a species eats, where it lives, how it behaves, and all the other aspects of its lifestyle.
- Chapter 10, p. 215

Tube Feet Water-filled tubes possessed only by echinoderms, many of which end in a sucker and can be extended and contracted to grip things and to move around.
- Chapter 7, p. 142

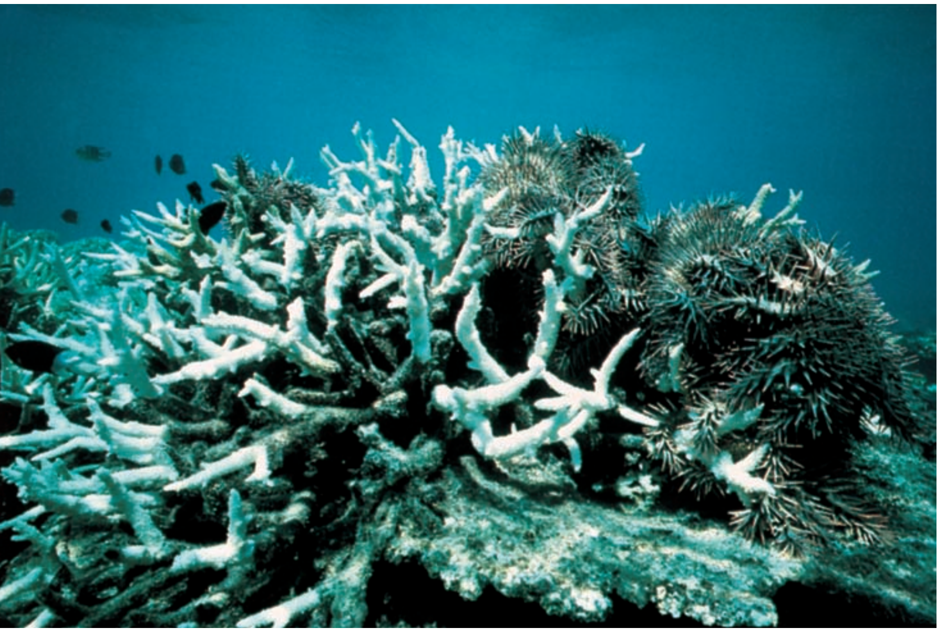


FIGURE 14.32 An outbreak of crown-of-thorns sea stars (*Acanthaster planci*) in Australia. The white branches of this colony of staghorn coral (*Acropora*) show the bare calcium carbonate skeleton left behind after being fed upon by several sea stars. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

dating back thousands of years, and in some places there are old stories and other historical evidence for past outbreaks. The outbreaks, then, may be a natural part of the reef ecosystem. A leading hypothesis is that in unusually wet years river runoff naturally brings more nutrients into the sea than normal. According to this hypothesis, the extra nutrients increase the growth of phytoplankton that are food for sea star larvae. It may also be that periodic population explosions are a natural part of the sea star's biology.

The evidence for past outbreaks of the crown-of-thorns, however, is hotly disputed. Some scientists are convinced that the plagues result from some human activity that has altered the ecological balance of reefs. Even if outbreaks did occur in the past, they seem to be happening more often. If occasional peaks in nutrient inputs cause natural outbreaks, nutrients from fertilizers, sewage, and other human sources may be making them worse. Another hypothesis is that fishers have caught too many fishes that eat young sea stars, allowing more to survive to adulthood. Some biologists have suggested that plagues occur because shell collectors have removed the triton shell, a large snail that preys on adult crown-of-thorns. Others argue that even without shell collectors the triton shell has always been naturally rare and unlikely to control sea star populations. They also point out that crown-of-thorns outbreaks continue to occur in areas where collecting triton shells has been banned for years.

The question of crown-of-thorns outbreaks has practical implications for the management and protection of reefs. If the outbreaks are caused by humans and threaten reefs, then we should probably try to do something to stop them. On the other hand, the "plagues" may be a natural, potentially important, part of the ecosystem. We might do more harm than good by interfering in a system we don't understand. The managers of the Great Barrier Reef have taken a middle road. They have developed an effective method to kill sea stars by injecting them with a poison. They use the poison, however, only if a crown-of-thorns outbreak is threatening a particularly valuable part of the reef, such as a popular dive spot or a scientific research site. Otherwise, they allow the outbreak to run its course.

> The crown-of-thorns sea star has undergone population explosions on many Pacific reefs. There is still debate about what causes the outbreaks and what should be done about them.

Grazing Grazing on algae by herbivores is at least as important in coral reef ecosystems as is predation on corals. Many fishes, especially surgeonfishes (*Acanthurus*), parrotfishes (*Scarus, Sparisoma*), and damselfishes (*Pomacentrus, Dascyllus*) graze intensively on reefs. Among the invertebrates, sea urchins (*Diadema, Echinometra*) are especially important. Many **microherbivores,** small invertebrates like snails, **chitons,** crustaceans, and polychaete worms, also eat algae.

Many seaweeds grow rapidly and can potentially outcompete and overgrow corals. Under natural conditions they are common on the reef (see "Coral Reef Seaweeds," p. 105), but are kept in check by grazers and nutrient limitation. Caging experiments (see "Transplantation, Removal, and Caging Experiments," p. 252) have been used to demonstrate the importance of grazers. For example, seaweeds are abundant on sand flats next to many Caribbean reefs but relatively scarce on the reef itself. To test the hypothesis that reef fishes were responsible for this, biologists transplanted seaweeds from the sand flat to the reef. If left unprotected, they were soon eaten by fishes. When protected by cages, they grew even faster than on the sand flat! The seaweeds are perfectly capable of living on the reef, therefore, but are rare there because they get eaten. Caging experiments on the Great Barrier Reef have had similar results.

If grazers are removed, seaweeds can flourish and take over space from corals and other organisms. In many parts of the Caribbean, for example, grazing reef fishes have become less common because of fishing. When this happened another important grazer, a sea urchin (*Diadema antillarum;* Fig. 14.33), became more common. The urchin apparently benefited from the reduced competition. For years, the urchin seems to have picked up the slack for the fishes, and seaweed populations remained

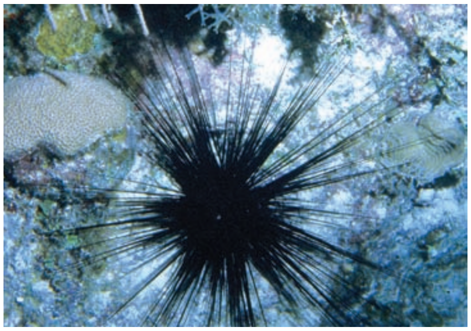


FIGURE 14.33 The long-spined black sea urchin (*Diadema antillarum*) is one of the most important grazers on Caribbean reefs. Closely related species are found on reefs in other parts of the world.

“Must Have Been Something I Ate”

Ahhhhh! You’re relaxing on a warm tropical night after a delicious fish dinner. The palm trees sway, a warm tropical breeze blows—and suddenly your bowels begin to churn. Before long your lips burn and tingle, and your hands and feet feel like pins and needles. You go into the kitchen for a drink, but the cool water feels warm. The cool floor and the cold compress you put on your forehead are also warm to the touch: The sensations of hot and cold are reversed. As you stagger to the bathroom, your arms and legs are heavy and weak. Now feeling really sick, you mumble, “Must have been something I ate.”

You’re right. What you have is a case of **ciguatera**—tropical fish poisoning. You’re not alone. Tens, perhaps hundreds, of thousands of people get ciguatera every year. And relax, you probably won’t die, though you might be a little sick (if you’re unlucky, *very* sick) for months or even years. Don’t count on a cure, though there are various folk remedies that might help a little. The intravenous administration of an inexpensive sugar called mannitol also helps sometimes.

So what *is* ciguatera, anyway? The disease has been known for hundreds of years. The name comes from the Spanish word for a Caribbean snail: You can also get ciguatera from eating molluscs, and perhaps sea urchins, though fish dinners are the most common cause. Ciguatera is caused by toxic dinoflagellates that live on the surface of seaweeds. Herbivorous fishes like surgeonfishes and parrotfishes ingest the dinoflagellates, and their toxins, along with the seaweeds. Predatory fishes like jacks, barracudas, and groupers pick up the toxin when they eat the herbivores. An intense, localized bloom of the dinoflagellates can mean that herbivorous fishes feeding in that spot become toxic, while fishes a short distance away are unaffected. If the dinoflagellates are widespread at relatively low levels, herbivorous fishes may remain safe, while predators that range over larger distances and eat many fish steadily accumulate toxins and become poisonous. Thus, it is hard to predict which fish are safe to eat, although certain species are known to have a higher risk than others. Which species are risky varies from place to place, so local knowledge is essential.

It is possible to tell if fish are affected—all you need is a laboratory. The toxins can be identified through chemical analysis, or by exposing test organisms such as mice or mosquito larvae to extracts. A simpler test is to feed a bit to a cat: Cats are highly sensitive to ciguatera. If any mongooses are handy, they’re good tasters, too. This isn’t very kind to the animals, who usually die if the fish carries ciguatera. Test sticks that change color when rubbed into the flesh of toxic fish have been developed but are not very reliable, sometimes indicating that toxic fish are safe and *vice versa.* This may be because there are at least 20 toxins involved, not just one, and it is hard to develop a test to reliably pick them all up in any combination. For now, at least, the best strategy is to avoid eating fish species that are known to be risky. Otherwise, it’s go hungry or take your chances.

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more or less stable. In 1983, however, a disease wiped out populations of the urchin over much of the Caribbean. Seaweeds, released from grazing pressure, became much more abundant on many reefs, at the expense of corals. In Jamaica they took over many reefs almost completely, and the formerly rich coral reefs are now more seaweed bed than coral reef.

Many reef scientists fear that such changes are becoming more and more common as fishing pressure on reefs escalates because of increasing populations and demand for tasty reef fish. There is often a double whammy. Coastal development often leads not only to more intensive fishing, but also to greater release of nutrients from sewage and agricultural fertilizer. Thus, seaweed growth may be artificially enhanced by eutrophication at the same time that the grazers that keep the seaweeds under control are removed. This is one of the main global threats to coral reefs.

Grazers help prevent fast-growing seaweeds from overgrowing other sessile organisms on the reef.

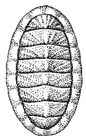
In addition to controlling how *much* algae there is, grazers affect which particular *types* of seaweed live on the reef and where. Coralline algae, for example, are abundant because the calcium carbonate in their tissues discourages grazers. Other seaweeds produce noxious chemicals that are poisonous or taste bad; these seaweeds also tend to be abundant. Seaweeds that lack such defenses are most heavily grazed and thus tend to be rare. Even so, they generally grow rapidly and are an important food source.

Damselfishes provide some interesting examples of the effects of grazing on reefs. Many damselfishes graze on seaweeds inside territories that they vigorously defend, chasing away other fishes that happen to venture inside. Many such damselfishes actually “farm” their territories. They weed out unpalatable algae, pulling them up and carrying them outside the territory. What is left in the territory is a dense mat of tasty seaweeds, usually fine, filamentous types. Protected by the damselfish, these algae grow very rapidly and outcompete corals and coralline algae. Outside the territory, parrotfishes and surgeonfishes gobble up the algae, clearing space for other organisms. Thus, the community inside the territory is very different from that outside. One interesting point is that cyanobacteria, which are nitrogen fixers, are more common inside damselfish territories than outside. Thus, damselfishes may indirectly have an important role in the nutrient balance of the reef.

Symbiosis Among the vast number of species that live on coral reefs, many have evolved special symbiotic relationships. There are far too many cases of symbiosis on the reef to describe here. In fact, coral reefs probably have more different symbiotic relationships than any habitat on earth. The few examples discussed here will give you some idea of how fascinating these relationships are.

Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface.

- Chapter 7, p. 132



Symbiotic relationships are very important in coral reef communities. Coral reefs probably have more examples of symbiosis than any other biological community.

We have already seen how mutualism between corals and their zooxanthellae is the essential feature of reef formation. Many other organisms also have photosynthetic symbionts. Sea anemones, snails, and giant clams (*Tridacna*) all harbor zooxanthellae. The "deal" between the two partners is the same as in corals: The zooxanthellae get nutrients and a safe place to live, and the host gets food. Giant clams grow so large (Fig. 14.34) because their zooxanthellae provide a constant food supply.

There are primary producers other than zooxanthellae that live inside reef animals. As mentioned previously, some sponges have cyanobacteria that fix nitrogen in addition to performing photosynthesis. Certain sea squirts house a photosynthetic bacterium called *Prochloron*. *Prochloron* is especially interesting because it may be similar to the symbiotic organisms that eventually became the chloroplasts of plants (see "From Snack to Servant: How Complex Cells Arose," p. 73).

Another important example of mutualism on the reef is the relationship between corals and the crabs, shrimps, and fishes that help protect them from the crown-of-thorns sea star and other predators. Most corals host a number of **facultative** and **obligate symbionts,** especially crustaceans. Some of the obligate symbionts are parasites and harm the coral, some are commensals and apparently have no effect on the coral, and some are mutualists that benefit the coral. It is often hard to tell which is which, because for most symbionts the nature of the relationship between coral and symbiont is not well understood. Those who study such organisms frequently revise their ideas as more information is obtained. The crabs that protect their coral from predators, for instance, were once thought to be parasites.

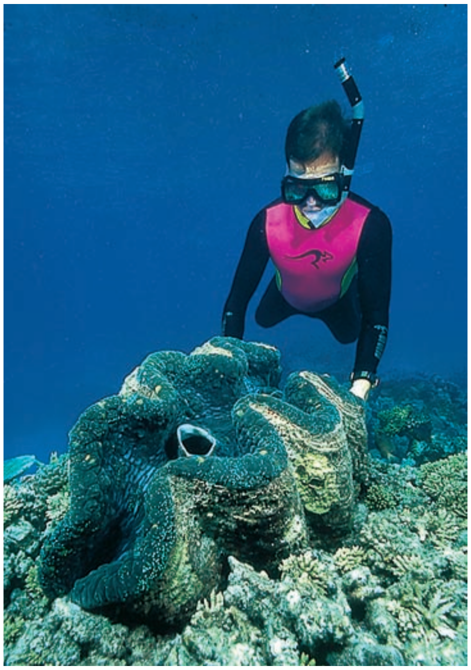


FIGURE 14.34 The giant clam (*Tridacna gigas*) does not deserve its reputation as a killer: Stories of people getting trapped in them and drowning are myths. Symbiotic zooxanthellae give the upper surface its blue and green colors, and provide food that allows the clam to get so big. The clam also filter-feeds. The hole visible on the clam's fleshy upper surface is one of the siphons through which it pumps water to feed and obtain oxygen. Giant clams do not occur in the Caribbean.

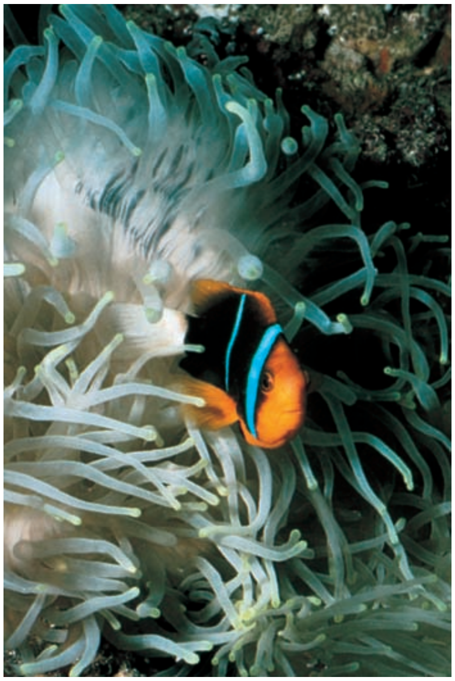


FIGURE 14.35 An orange-fin anemonefish (*Amphiprion chrysopterus*) and its sea anemone host.

Anemonefishes (*Amphiprion;* Fig. 14.35) have an interesting relationship with several kinds of sea anemones. The anemones inhabited by anemonefishes have a powerful sting and are capable of killing the fish. The fish have a protective mucus, however, that keeps the anemone from stinging. It is not known whether mucus is produced by the fish themselves, by the anemone, or by both. When anemonefishes are newly introduced to an anemone, they typically rub against and nip the anemone's tentacles. They may be coating themselves with the anemone's mucus. To understand why this is an advantage, you have to remember that anemones have no eyes and no brain, but lots of tentacles. If the anemone simply stung everything it touched, it would end up stinging itself every time the tentacles bumped into each other. The anemone recognizes itself by the "taste" of its own mucus. When one tentacle touches another, the anemone detects the mucus coating on the tentacles and refrains from stinging. Anemonefishes may be taking advantage of this. On the other hand, there is evidence that the fishes' own mucus protects them against the anemone, and in some cases the fish can enter an anemone unharmed without having ever contacted it before.

Anemonefishes are protected by the anemone's stinging tentacles and brood their eggs under the anemone. The anemone also benefits. Anemonefishes drive away other fishes that eat anemones, and also seem to benefit their hosts nutritionally. Anemones with anemonefish survive longer, grow faster, and reproduce by asexual division more often than anemones whose anemonefish are experimentally removed. Anemonefishes in aquaria sometimes feed their host. That doesn't seem to happen in nature, but host anemones might get scraps of food dropped by their symbionts. The anemones also have symbiotic zooxanthellae, which might benefit from nutrients in the anemonefish's waste products and pass some of the benefit on to the anemone. It has also been hypothesized that the anemone can occupy exposed locations to get more light for their zooxanthellae because the anemonefish protect the anemone from predators. As with most aspects of coral reef ecology, there is still much to learn.

Facultative Symbiont A symbiont that is not completely dependent on its partner and can live outside the symbiosis.
Obligate Symbiont One that depends on its partner and does not occur outside the symbiosis.
- Chapter 10, p. 219

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. What factors might account for the fact that the vast majority of atolls occur in the Indian and Pacific oceans and that atolls are rare in the Atlantic?
2. Scientists predict that the ocean will get warmer and the sea level will rise as a result of an intensified greenhouse effect (see "Special Report: Our Changing Planet," p. 231). How might this affect coral reefs?
3. There are only a few reefs off the northeast coast of Brazil (see map in Fig. 14.11), even though it lies in the tropics. How would you explain this?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

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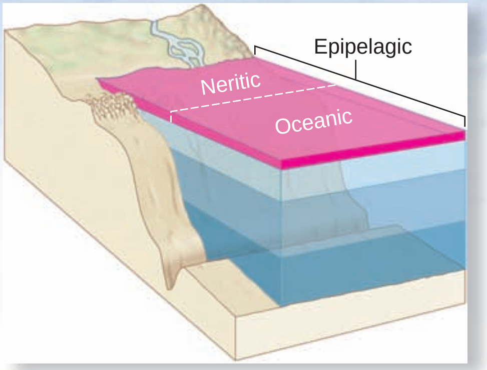
15

CHAPTER

Life Near the Surface



A blue shark (*Prionace glauca*) hunts its prey.

"The ocean," for most of us, conjures up images of beaches and cliffs, breaking surf, or quiet bays. Such familiar nearshore waters, however, make up only a small fraction of the world ocean. The rest is the vast open sea, the **pelagic realm.** Though distant and unfamiliar, the open ocean affects us all. It regulates our climate, conditions our atmosphere, and provides food and other resources. It is hard for most of us to really grasp how vast the pelagic realm is. It holds practically all the liquid water on earth, the water planet.

The pelagic environment is the water column itself, away from the bottom or the shore. Pelagic organisms live suspended in their liquid medium. With few exceptions, the pelagic lacks the solid physical structure provided either by the bottom and other geological features or by large organisms like corals and kelps. There is no place for attachment, no bottom for burrowing, nothing to hide behind. Imagine spending your life floating weightless in the air, never touching the ground. This is what the pelagic realm is like for the organisms that live there.

Chapter 15 deals with the surface layers of the pelagic environment: the **epipelagic,** or upper pelagic, realm. The epipelagic is often defined as the zone from the surface down to a given depth, commonly 200 m (650 ft). Being the shallowest part of the pelagic realm, the epipelagic is generally the warmest, and, of course, the best lit. The epipelagic is therefore similar to the **photic zone,** the zone from the surface to the depth where there is no longer enough light for organisms to grow by photosynthesis. The depth of the photic zone varies, depending on water clarity and the amount of sunlight. In practice the epipelagic and photic zones are usually much the same, and their differences will not be stressed in this chapter.

The epipelagic is divided into two main components. Epipelagic waters that lie over the continental shelf are referred to as **neritic** (see Fig. 10.12). The neritic environment is only a small part of the epipelagic, but it is important to humans because it lies relatively close to shore and supports most of the world's marine fisheries production (see "Major Fishing Areas," p. 381). The surface waters beyond the continental shelf are known as the **oceanic** part of the epipelagic.

The epipelagic realm is the layer of the ocean from the surface to a depth of 200 m. It is divided into neritic waters, which lie over the continental shelf, and oceanic waters beyond the shelf. The epipelagic is similar to the photic zone, the layer from the surface to the depth where light limits photosynthesis.

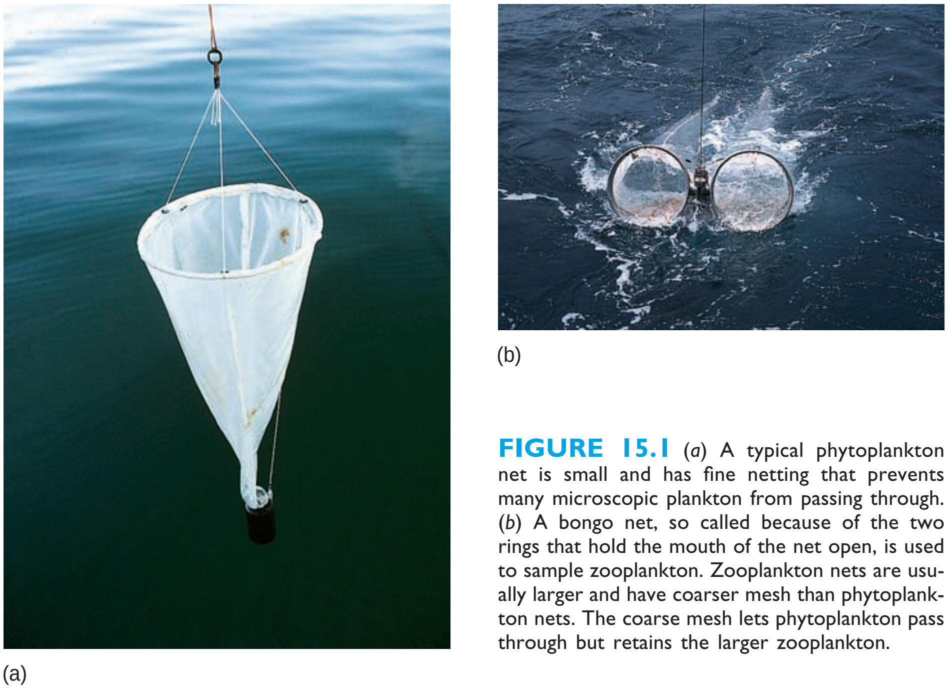


FIGURE 15.1 (*a*) A typical phytoplankton net is small and has fine netting that prevents many microscopic plankton from passing through. (*b*) A bongo net, so called because of the two rings that hold the mouth of the net open, is used to sample zooplankton. Zooplankton nets are usually larger and have coarser mesh than phytoplankton nets. The coarse mesh lets phytoplankton pass through but retains the larger zooplankton.

THE ORGANISMS OF THE EPIPELAGIC

Like nearly all ecosystems, the pelagic realm is fueled by solar energy captured in photosynthesis. Epipelagic ecosystems differ from many shallow-water ones in that nearly all the **primary production** takes place within the epipelagic system itself. Coastal ecosystems often receive large amounts of food from elsewhere. The intertidal zone, for example, gets plankton and drifting seaweeds from offshore, and rivers carry organic material into estuaries. The pelagic realm, far from the shore and bottom, gets almost no external input of organic matter.

The epipelagic does supply food to other communities. Large amounts of organic matter sink out of the epipelagic to feed the organisms below (see Chapter 16). Ocean currents carry epipelagic **plankton** into shallow water, where it is consumed by a profusion of **suspension feeders.** Epipelagic fishes and zooplankton provide food not only to other marine communities, but also to land-dwelling birds and mammals, including humans.

Because there is no bottom where organic-rich sediments can build up, the epipelagic lacks **deposit feeders.** Suspension feeders, on the other hand, abound. After all, the food is suspended in the water column. There are also many large predators, like fishes, squids, and marine mammals.

The Plankton: A New Understanding

For more than a century the main way that scientists studied the plankton was to catch them by towing nets through the water (Fig. 15.1), or sometimes by pumping water through a filter. This reliance on plankton nets profoundly affected our understanding of the epipelagic. Imagine if our only way to study flying organisms was with nets. If our nets were too small or too slow, we might never know there were birds. Nets with too coarse a mesh would leave us completely ignorant of mosquitoes. Imagine organisms with the consistency of clouds that slipped through any net! Similar misunderstandings resulted from oceanographers' dependence on plankton nets to study the epipelagic.

In recent decades, new techniques including better microscopes, underwater photography, satellites, chemical procedures, and, yes, even improved nets and filters, have revolutionized our understanding of the epipelagic. New discoveries have raised even more questions, and it has become clear that we don't understand the plankton nearly as well as we once thought.

Of particular importance was the discovery of vast numbers of plankton that are too small to be caught in standard plankton nets. These are often subdivided on the basis of the size (Fig. 15.2). The **femtoplankton** is composed almost entirely of **viruses** and is often also called the **virioplankton.** Most of the **picoplankton** consists

Primary Production The conversion of carbon dioxide (CO_2) into organic matter by autotrophs, that is, the production of food.
- Chapter 4, p. 68

Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Deposit Feeders Animals that eat organic matter that settles to the bottom.
Suspension Feeders Animals, including *filter feeders,* that eat particles suspended in the water column.
- Chapter 7, p. 116; Figure 7.3

Viruses Particles composed of nucleic acids and proteins that are not usually considered to be alive.
- Chapter 4, p. 82; Chapter 5, p. 86

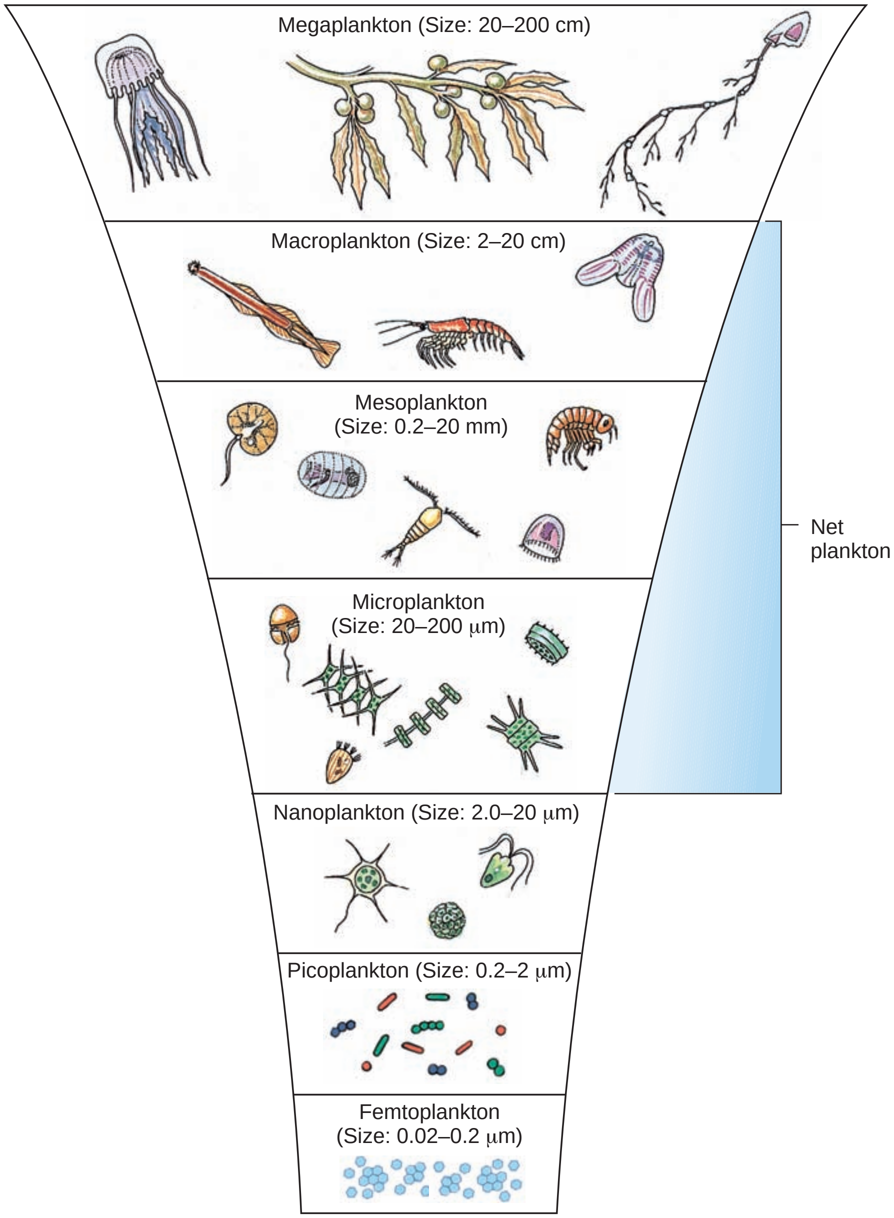
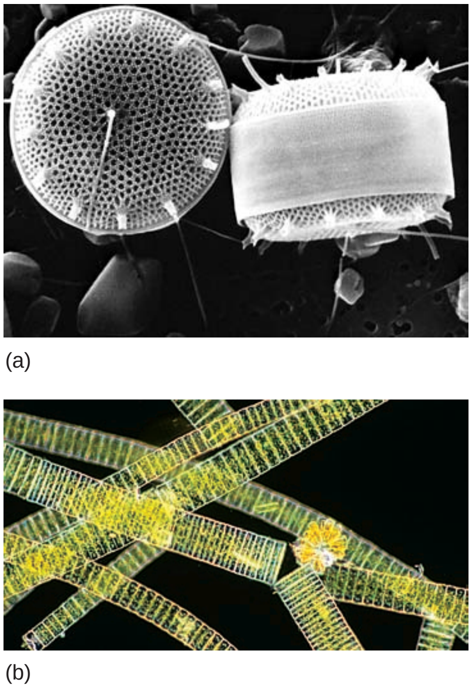

Megaplankton (Size: 20–200 cm)
Macroplankton (Size: 2–20 cm)
Mesoplankton
(Size: 0.2–20 mm)
Microplankton
(Size: 20–200 μm)
Nanoplankton (Size: 2.0–20 μm)
Picoplankton (Size: 0.2–2 μm)
Femtoplankton
(Size: 0.02–0.2 μm)
Net
plankton

FIGURE 15.2 Plankton are often separated into categories based on their size (also see Appendix A). Note that the size of the organisms in each category increases logarithmically, that is, the size range of each category is ten times that of the next smaller category.


(a)

(b)

FIGURE 15.3 Diatoms have sculptured shells, or frustules, made of silica. (*a*) *Thalassiosira allenii* (top and side views) consists of a single cell. (*b*) Fragillaria is a diatom that forms chains of cells. Each division in the long, green filaments is an individual cell (also see Fig. 5.5).

of **archaea** and **bacteria.** The larger **net plankton,** so called because they *can* be caught in nets, are also subdivided on the basis of size into the **micro-, meso-, macro-,** and **megaplankton,** but these categories are not stressed in this book. Categorizing the plankton by size should not be confused with the division between **phytoplankton**—plankton that perform photosynthesis—and **zooplankton.** The phytoplankton, for example, include species of all size classes from the picoplankton to the megaplankton.

The Phytoplankton

Large producers like seaweeds and seagrasses are largely absent from the epipelagic because they have no place to attach. Floating seaweeds are important in a few places, like the Sargasso Sea (see Fig. 8.24), but in most of the epipelagic the only primary producers are single-celled or simple chains of cells. These tiny organisms make up the phytoplankton, which occur virtually everywhere in the epipelagic, often in huge numbers. Phytoplankton perform more than 95% of the photosynthesis in the ocean. This amounts to nearly half the world's primary production and produces nearly half the oxygen in our atmosphere.

Because net phytoplankton are relatively easy to catch, their importance has long been known. Most important among these are **diatoms** (Fig. 15.3) and **dinoflagellates.** Before the discovery of the nanoplankton and picoplankton, it was thought that diatoms dominated the phytoplankton and accounted for most photosynthesis in the epipelagic. Although we now know this is not true, diatoms are still extremely important. They are especially common in temperate and polar regions and other nutrient-rich waters. They are abundant both near the coast and in the open ocean.

Dinoflagellates are another major group of net phytoplankton. They are important in both neritic and oceanic waters but tend to prefer warm areas. In the tropics they often replace diatoms as the most abundant members of the net phytoplankton. Dinoflagellates may be better-adapted to low-nutrient conditions than diatoms. Given nutrients, on the other hand, dinoflagellates may **bloom,** or grow explosively into huge numbers, sometimes causing **red tides** (see “Red Tides and Harmful Algal Blooms,” p. 334).

A group of **cyanobacteria,** *Trichodesmium,* grows in filamentous colonies that can be caught in nets. It can be very abundant, sometimes forming red tides. It is particularly abundant in nutrient-poor waters, perhaps because it can fix nitrogen (see “Nutrients,” p. 346).

Because they are so small and hard to catch, or even to see under a microscope, photosynthetic picoplankton and nanoplankton are not as well known as the net phytoplankton, and their great importance has only recently been appreciated. Photosynthetic picoplankton and nanoplankton are far more abundant than the net phytoplankton and contribute most of the epipelagic’s photosynthesis, 90% or more in many places.

Cyanobacteria are the most abundant picoplankton and account for at least half the ocean’s total primary production. One group, the single-celled *Prochlorococcus,* is the most abundant of all marine phytoplankton and is especially dominant in nutrient-poor tropical and subtropical waters. The closely related *Synechococcus* is also very abundant in all but polar waters.

Although cyanobacteria dominate the photosynthetic picoplankton, various protists are also important. These **eukaryotes** typically make up less than 5% of the total picoplankton cells in the water, but have been known to account for over 30% of picoplankton cells. An ample supply of nutrients appears to favor the increased abundance of protists relative to cyanobacteria. Many of the photosynthetic protists in the picoplankton have not been isolated and are known only from the presence of characteristic nucleic acid sequences in the water (see “Tiny Cells, Big Surprises,” p. 92). Their ecological role in the phytoplankton is poorly known.

Although protists have an uncertain role in the picoplankton, they dominate the nanoplankton, and many of them are photosynthetic. **Coccolithophorids** are one of the more abundant groups, and probably the best known. They do best in the open ocean but also occur in coastal waters.

Another group of minute phytoplankton known as **cryptophytes** are very plentiful in neritic waters. They appear to be very important in the economy of the seas, but not much is known about them. **Silicoflagellates** (see Fig. 5.9) occasionally bloom and become important primary producers. Several other groups of protistan nanoplankton appear to be important primary producers in the epipelagic. Although most diatoms and dinoflagellates belong to the net plankton, a few unusually small species are part of the nanoplankton.

Phytoplankton are the main primary producers in the epipelagic. The most abundant phytoplankton are cyanobacteria and various groups of protistan pico- and nanoplankton, including coccolithophorids, cryptophytes, and silicoflagellates. Among the larger net phytoplankton, diatoms and dinoflagellates are dominant.

Table 15.1 shows the major groups of marine phytoplankton. Various other groups may form blooms, but relatively rarely, and are of secondary importance in the overall economy of the seas.

The Zooplankton

Phytoplankton form the base of the food web. The solar energy that they capture and store in organic matter is passed on to the other creatures of the epipelagic, from minute zooplankton to gigantic whales. The first step in this flow of energy occurs when **herbivores** eat the phytoplankton. Herbivores are the vital link between the primary producers in the phytoplankton and the rest of the community. Large epipelagic animals cannot feed directly on the tiny phytoplankton. They rely instead on herbivorous zooplankton, which can. Thus, a fundamental part of the epipelagic food web is the flow of energy from phytoplankton to herbivorous zooplankton.

Very few zooplankton are strict herbivores and those that eat phytoplankton also eat other zooplankton occasionally. Most zooplankton species are primarily carnivorous and hardly eat phytoplankton at all. These carnivores may feed directly on herbivorous zooplankton and thus reap the production of phytoplankton with only one intermediate step, or **trophic level,** in the food web. They may also eat other carnivores, adding links to the food web (Fig. 15.4).

Protozoan Zooplankton The tiny picoplankton and nanoplankton are too small for most multicellular animals to catch and eat. **Protozoans,** however, can catch them. When it was discovered that pico- and nanoplankton are the most abundant phytoplankton, the importance of protozoans was also recognized. Without protozoans, much of the primary production in the epipelagic would go unutilized. The most important of these protozoans are various **flagellates,** protozoans that move around by means of flagella. **Ciliates, foraminiferans** (Fig. 15.5), and **radiolarians** (see “Protozoans: The Animal-Like Protists,” p. 98) are also important protozoan grazers, on net plankton as well as pico- and nanoplankton. Many grazing protozoans are capable of photosynthesis, so they also act as members of the phytoplankton.

Archaea Single-celled, *prokaryotic* organisms once thought to be bacteria but now known to be as different from bacteria as from humans.
- Chapter 5, p. 89

Dinoflagellates Single-celled organisms that use two flagella to swim.
- Chapter 5, p. 95

Nitrogen Fixation The conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.
- Chapter 5, p. 93; Table 5.1

Eukaryotes Organisms with cells that contain a nucleus and other organelles that are enclosed by membranes.
- Chapter 4, p. 69; Figure 4.8

Protozoans Single-celled organisms that are animal-like in that they ingest food and usually can move around.
- Chapter 5, p. 97

Table 15.1 The Major Groups of Marine Phytoplankton

Size Category	Group	Neritic or Oceanic	Latitude/Temperature	Notes
Net plankton	Diatoms	Both	Everywhere, but most common in temperate and polar waters	Important primary producers
	Dinoflagellates	Both	Everywhere, but most common in warm waters	Common red tide organisms
	Colonial cyanobacteria (*Trichodesmium*)	Oceanic	Mainly tropical	Can fix atmospheric nitrogen; causes red tides in the Red Sea
Nanoplankton	Coccolithophorids	Oceanic	Everywhere, but most common in tropical waters	Important primary producers in nutrient-poor waters
	Cryptophytes	Both	Everywhere, but most common in temperate and polar waters	Very important primary producers; poorly known
	Silicoflagellates	Neritic	Temperate and polar waters	Sometimes form blooms
Picoplankton	Unicellular cyanobacteria (*Prochlorococcus, Synechococcus*)	Both	Everywhere, but most important in warm waters	Dominant primary producers, especially in nutrient-poor waters
	Various protists	Not known	Not known	Presence of many groups recently discovered

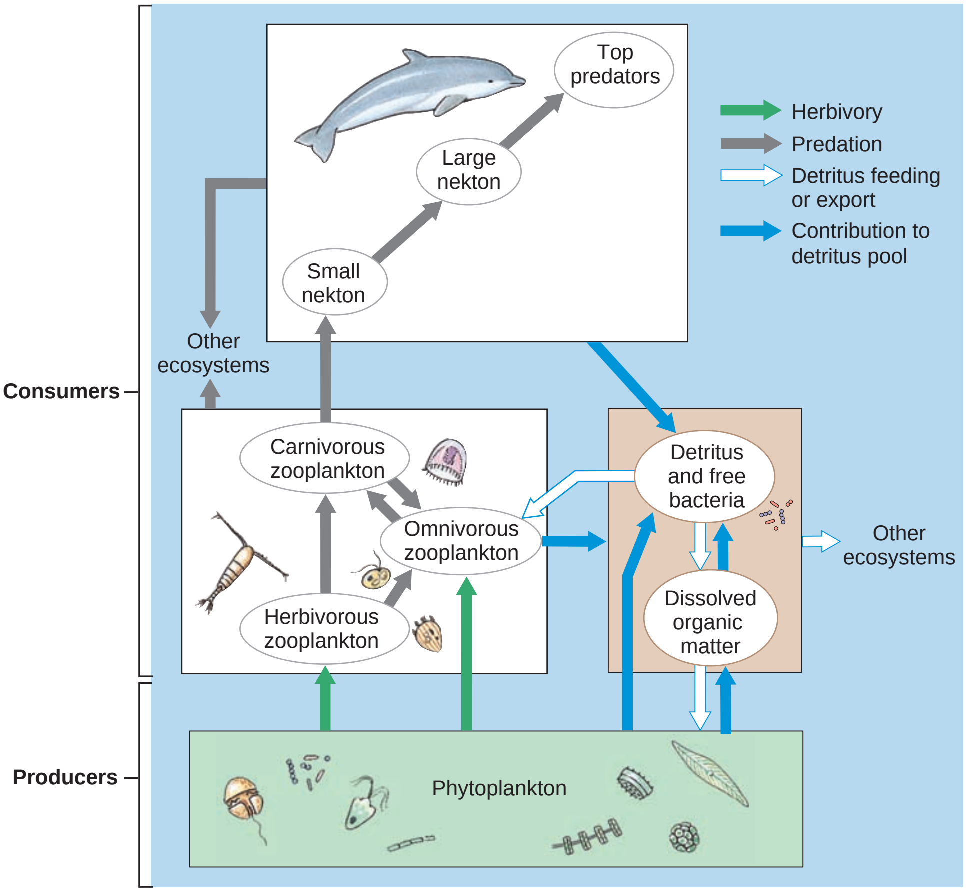

Top predators
Large nekton
Small nekton
Other ecosystems
Consumers
Carnivorous zooplankton
Omnivorous zooplankton
Herbivorous zooplankton
Detritus and free bacteria
Dissolved organic matter
Other ecosystems
Producers
Phytoplankton
Herbivory
Predation
Detritus feeding or export
Contribution to detritus pool

FIGURE 15.4 A simplified epipelagic food web.

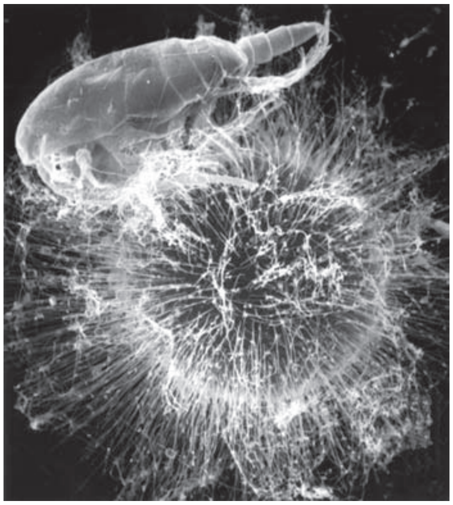


FIGURE 15.5 A planktonic foramaniferan (*Orbulina universa*) captures a copepod on its long, sticky pseudopodia. The copepod will be drawn to the surface of the foram's shell, where it will be digested. The shell is 0.5 mm (0.02 in) in diameter.

Copepods Small crustaceans, especially **copepods** (Fig. 15.6), dominate the net zooplankton. Copepods are the most abundant members of the net zooplankton practically everywhere in the ocean, typically numbering 70% or more of the community. This probably makes them the most numerous group of animals on earth.

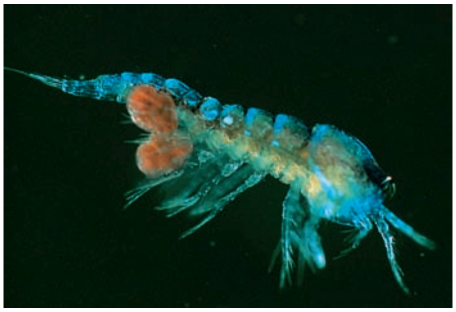


FIGURE 15.6 An epipelagic copepod. The orange balls attached to the tail are eggs (also see Fig. 7.28).

Nearly all epipelagic copepods eat at least some phytoplankton. It was once thought that they use the bristles on their mouthparts and antennae (Fig. 15.7*a*) to sieve phytoplankton cells out of the water, eating whatever particles happen to be the right size to snag in the bristles. In fact, this is not the case. For small organisms like copepods, water is much more viscous, or syrupy, than it seems to us. The bristly appendages of copepods act more like paddles than sieves, and are used to create water currents that draw individual phytoplankton cells close enough for the copepod to grab. At least some copepods can sense individual phytoplankton cells, using both sight and smell, and actively select cells to eat rather than passively consuming whatever happens to get caught on their appendages.

Copepods are also major carnivores. Though most copepods eat at least some phytoplankton, many also eat other zooplankton, including other copepods, when they can. A few copepods are exclusively carnivorous. These generally catch their prey by seizing it with their claw-like appendages (Fig. 15.7*b*).

Other Crustaceans Other crustaceans are also important members of the zooplankton. Though not as abundant globally as copepods, shrimp-like **krill** often aggregate into huge, dense swarms. Preferring cold oceanic waters, krill sometimes dominate the zooplankton in polar seas. They are efficient filter feeders, capturing phytoplankton, especially diatoms, with their bristly appendages. Krill also eat small zooplankton and **detritus** including fecal pellets, the solid waste excreted by other zooplankton.

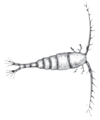
Copepods are so small that most large animals can't catch them. Krill, by contrast, are relatively big, up to 6 cm (2.5 in) in Antarctic krill (*Euphausia superba;* see Fig. 17.12). Fishes, seabirds, and even great whales eat them (see Fig. 10.14).

Although copepods and krill are by far the most abundant, there are many other crustaceans in the zooplankton, both herbivorous and carnivorous. At certain times and places, one of these crustacean groups may be very abundant. Amphipods and most other planktonic crustaceans are small, like copepods. A few larger crustaceans, also occur in the net zooplankton. These include a number of decapods—crabs, shrimps, and their relatives (see "Shrimps, Lobsters, and Crabs," p. 136). The decapods are almost exclusively carnivorous.

Copepods, krill, and other crustaceans dominate the net zooplankton. Copepods are the main herbivores in the epipelagic and are by far the most abundant group of zooplankton.

Non-Crustacean Zooplankton The zooplankton includes many animal groups other than crustaceans. **Salps** (Fig. 15.8) are transparent, planktonic relatives of the sea squirts, or tunicates, that live on the bottom (see "Tunicates," p. 146). Salps catch phytoplankton by filtering water through a sieve-like sac or a fine mucus net.

Copepods Tiny crustaceans that are often planktonic.
- Chapter 7, p. 135



Krill Planktonic, shrimp-like crustaceans.
- Chapter 7, p. 136

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

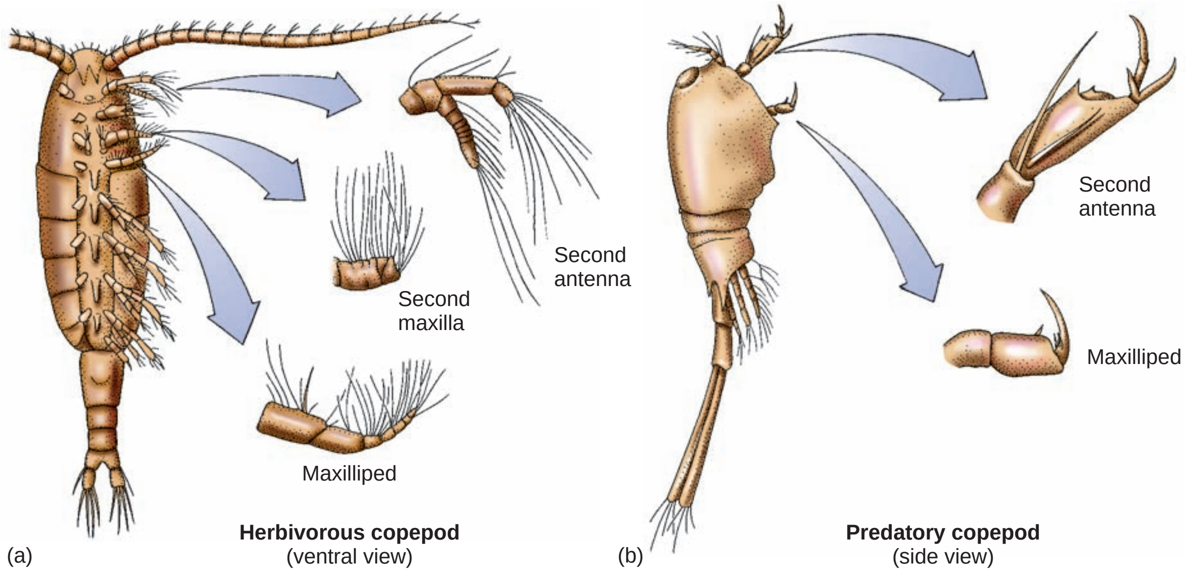


FIGURE 15.7 (*a*) The mouthparts and appendages of copepods that feed mainly on phytoplankton, such as Calanus, have many long bristles. (*b*) Copepods that prey on other zooplankton, such as *Corycaeus,* have appendages with fewer and shorter bristles. Their appendages are better adapted for grasping.

Red Tides and Harmful Algal Blooms

From time to time, especially near the coast, the sea becomes bright red literally overnight. This phenomenon, called a red tide, has occurred for thousands of years. The Old Testament (Exodus 7:20–21) may contain the earliest known reference to a red tide when it describes the waters of the Nile turning to blood. The Red Sea is named for the red tides that often occur there.

The term "red tide" is here to stay, but it is misleading. Red tides have nothing to do with the tide. They are massive blooms of phytoplankton. At the peak of a red tide there may be tens or hundreds of thousands of cells in a single drop! Furthermore, red tides aren't always red. The sea may instead turn orange, brown, or bright green. In fact, the name "red tide" is applied to harmful phytoplankton blooms even if they don't discolor the water. The term "brown tide" is sometimes used for blooms of phytoplankton called chrysophytes, but the basic phenomenon is the same.

Red tides are different from ordinary phytoplankton blooms like the spring bloom that occurs in cold waters (see "Seasonal Patterns," p. 349). The spring bloom includes many different species and is predictable, occurring in response to increased light or nutrient levels. Red tides, by contrast, are usually blooms of a single species and are unpredictable because we don't understand what causes them.

Only around 6% of all phytoplankton species are known to cause red tides. This may not sound like much, but it is still at least 200 species. About half are dinoflagellates, but many other organisms, including cyanobacteria, diatoms, and chrysophytes, can cause red tides.

Red tides are often nothing more than oceanographic oddities, but sometimes they cause problems. **Harmful algal blooms (HABs)** are receiving increasing attention from both scientists and society at large. Of course, what is harmful depends on your point of view. If you are on a beach vacation, a foul brown foam caused by a bloom may be nothing more than an annoying reason to cut the vacation short. To the motel owner depending on your business it is a disaster.

Some blooms are more than just a nuisance. They are deadly. About a third of red tide organisms produce poisons, including some of the most powerful toxins known. Normally there are too few of the organisms around to worry about, but when they bloom they can cause serious problems. Mussels, clams, crabs, and other shellfish often tolerate the toxins by storing them away in the digestive gland, kidney, liver, or other tissues. People who eat the shellfish can suffer nausea, diarrhea, vomiting, numbness and tingling, loss of balance and memory, slurred speech, shooting pains, paralysis, and even death. Toxic algae cause an estimated 100,000 to 200,000 cases of serious poisoning a year, including ciguatera (see '"Must Have Been Something I Ate,"' p. 325). These lead to 10,000 to 20,000 deaths and a similar number of cases of paralysis and other consequences. You don't have to eat shellfish to suffer. Swimming or boating in affected water, even breathing sea spray, can cause sore throats, eye irritation, and skin complaints. Some of the toxins may be carcinogenic.

A bloom of a dinoflagellate called *Noctiluca* caused this red tide in Mexico. The organism is bioluminescent, and blooms like this produce spectacular blue-green light at night.

Larvaceans (Fig. 15.9) are also relatives of sea squirts, though they hardly look it—except for their larvae. Sea squirt larvae, known as tadpole larvae, are very similar to larvaceans (see Fig. 7.51*b*). Larvaceans float inside a "house" they make of mucus. By beating its tail, the larvacean pumps water in through passages in the house. Food particles are caught in a mucus net that is secreted inside the house. At least some larvaceans also secrete a net outside the house that can extend as far as 2 m (6 ft). The use of sticky mucus nets allows larvaceans to capture extremely small food particles. Larvaceans and some salps are among the few animals that can catch pico- and nanoplankton. They are therefore important in linking primary production by pico- and nanoplankton to the rest of the epipelagic community.

The openings through which water enters the house filter out particles too large for the larvacean to eat. These filters eventually get clogged. Some species can reverse the water flow to clear the filters. If the filters get too clogged or a predator threatens, the larvacean simply abandons the house and swims away. It can produce a new house within minutes and resume feeding. When disturbed, some species can build and discard houses every 10 minutes! Even under normal circumstances, most species change houses every four hours or so. Discarded houses are an important source of detritus and transport large amounts of carbon to the deep sea as they sink. (see "Gelatinous Zooplankton and Carbon Flux to the Deep Sea," p. 372).

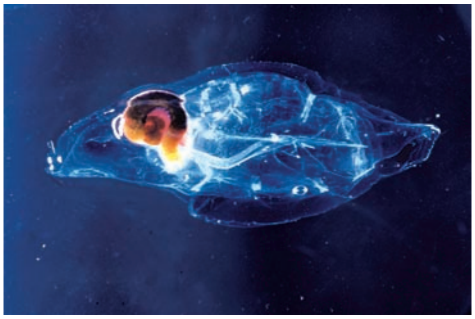


FIGURE 15.8 A pelagic salp (*Salpa thompsoni*) from Antarctica. These gelatinous animals feed by filtering phytoplankton out of the seawater. Like larvaceans (Fig. 15.9), some of them are able to capture bacteria and other very tiny plankton.

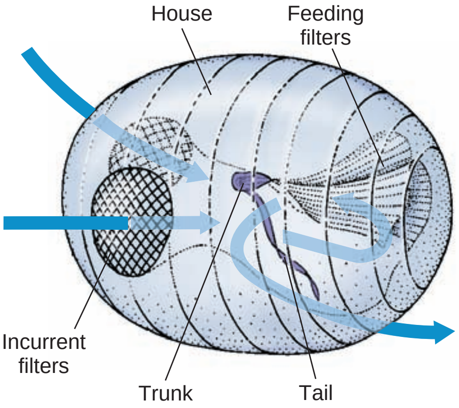


FIGURE 15.9 A larvacean spends most of its time inside a mucus "house." By beating its tail, the larvacean draws water into the house (blue arrows) through two intake filters. Food particles are caught on the mucus feeding net, and the filtered water flows outward.

The effects of HABs aren't confined to humans. HABs can turn the surface into a sea of dead fish. In recent years a dinoflagellate called *Pfiesteria* has been a particular problem along parts of the U.S. east and Gulf coasts (see "Dinoflagellates," p. 106), but many other HAB organisms cause fish kills. Whales and sea birds that eat fish have also been killed. Even herbivores have been affected. Though they eat aquatic vegetation, Florida manatees have been killed by red tides on several occasions. They are exposed just by being in the water, and perhaps by breathing toxic spray at the surface. In 1996 about 150 manatees, or 10% of the small surviving population, were killed by red tides.

The harmful effects of algal blooms are not always caused by toxins. Blooms of some diatoms kill fish because the diatoms' sharp spines damage the fishes' gills. Even when algae don't harm fish directly, their blooms can cause fish kills when the masses of phytoplankton die, their decomposition depletes the water of oxygen, and the fish suffocate. Phytoplankton may harbor the bacteria that cause cholera, a deadly disease, implicating phytoplankton blooms in cholera epidemics.

Red tides cost hundreds of millions of dollars in losses to fisheries and tourism. Valuable shellfish beds are often closed because of red tides, or during seasons when red tides are likely. Perfectly safe seafood may be rendered nearly worthless if the public perceives it as dangerous. Fish farms and other aquaculture facilities are especially vulnerable because the fish or other seafood can't swim away and because they are usually held in high densities. The cost of HABs is estimated at $49 million annually just in the United States, and is many times higher globally.

HABs have been around since long before biblical times. There is fossil evidence of red tides from more than 100 million years ago. Scientists are concerned, however, that they seem to be becoming more common. It is hard to be sure: IT may just be that HABs are more obvious. With more people living on the coast, it is more likely someone will get sick if an HAB occurs, and scientific advances make it easier to tell why they got sick. Where a bloom might go unnoticed in a lonely, undeveloped bay, it is devastatingly obvious once an aquaculture industry has been established.

Still, there is good evidence that HABs are increasing as a result of human activity. In Hong Kong and the Seto Inland Sea in Japan, for example, HABs steadily became more common as the population and water pollution increased. In the Seto Inland Sea the case is even stronger: HABs declined again after pollution control measures were introduced.

If humans *are* causing more HABs, the most likely cause is **eutrophication,** increased algal growth due to nutrient pollution. This might lead to more frequent red tides, some of which will be HABs. Furthermore, eutrophication might selectively favor harmful algae. Humans don't add the same nutrients to the ocean that nature does. We add a lot of nitrogen (N) (see "Overwhelming the Nitrogen Cycle," p. 236), and less phosphorus (P) and silicon (Si). Dams also reduce the supply of phosphorus and silicon. Most marine systems are nitrogen-limited, and when nitrogen is added the phytoplankton grow until they run out of something else. In particular, diatoms can run out of silicate, which they need to make their shells. This shifts the balance in favor of dinoflagellates. While some diatoms produce toxins, dinoflagellates are much more likely to do so. Not only that, some dinoflagellates produce more toxin when their supply of phosphorus runs low, which is likely to happen if we pump in nitrogen and not phosphorus.

HABs are also spreading to new places. Ships can transport HAB organisms in their ballast water. A single ship was estimated to carry more than 300 million toxic dinoflagellate cysts! There is strong evidence that HAB organisms in Australia and New Zealand, for example, were introduced in ballast water. Natural movements of red tide organisms, though, are probably more important. The closure of shellfish beds in Canada and New England, for example, began when a hurricane carried in a seed population of toxic dinoflagellates. Red tide toxins have been turning up in shellfish there ever since.

A group of molluscs called **pteropods** also includes phytoplankton grazers. Pteropods are small snails in which the foot has been modified to form a pair of "wings" that they flap to stay afloat (Fig. 15.10). Some feed by capturing phytoplankton, including picoplankton and nanoplankton, in mucus nets or threads; others are carnivorous.

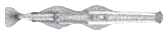
Larvaceans, salps, and some pteropods feed with mucus nets or threads. They are among the few zooplankton that can eat pico- and nanoplankton. Discarded larvacean houses are an important source of detritus in the epipelagic.

Arrow worms, or **chaetognaths** feed mostly on copepods. This may not be because they actually prefer copepods but because there are so many copepods around. Arrow worms consume an assortment of other prey when it is available. They can be very abundant, and have a major role in epipelagic food webs.

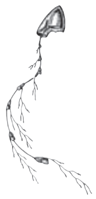
Not all carnivorous zooplankton are small. Jellyfishes and **siphonophores,** for example, can be quite large but are weak swimmers and drift with the currents as part of the plankton. Jellyfishes are carnivorous, and many eat small fishes as well as zooplankton. The somewhat similar **comb jellies** (see Fig. 15.19*b*) are also carnivorous. The ocean sunfish (*Mola mola*), which grows to 2,300 kg (5,000 lb), swims weakly and is sometimes considered a member of the zooplankton.

Meroplankton The zooplankton discussed so far, for except a few jellyfishes, spend their whole lives in the plankton and are called **holoplankton.** In addition to these permanent members of the zooplankton, there are a vast number of organisms that have planktonic larvae. These animals—whether from estuaries, the rocky intertidal, kelp beds, coral reefs, or even

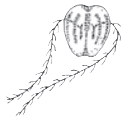
Arrow Worms or **Chaetognaths** Small, worm-like predators with fins along the body and spines on the head.
- Chapter 7, p. 140



Siphonophores Drifting colonial cnidarians in which different members of the colony are specialized for different tasks.
- Chapter 7, p. 120



Comb Jellies or **Ctenophores** Radially symmetrical animals that resemble jellyfishes but have eight rows of cilia and no *nematocysts*.
- Chapter 7, p. 122



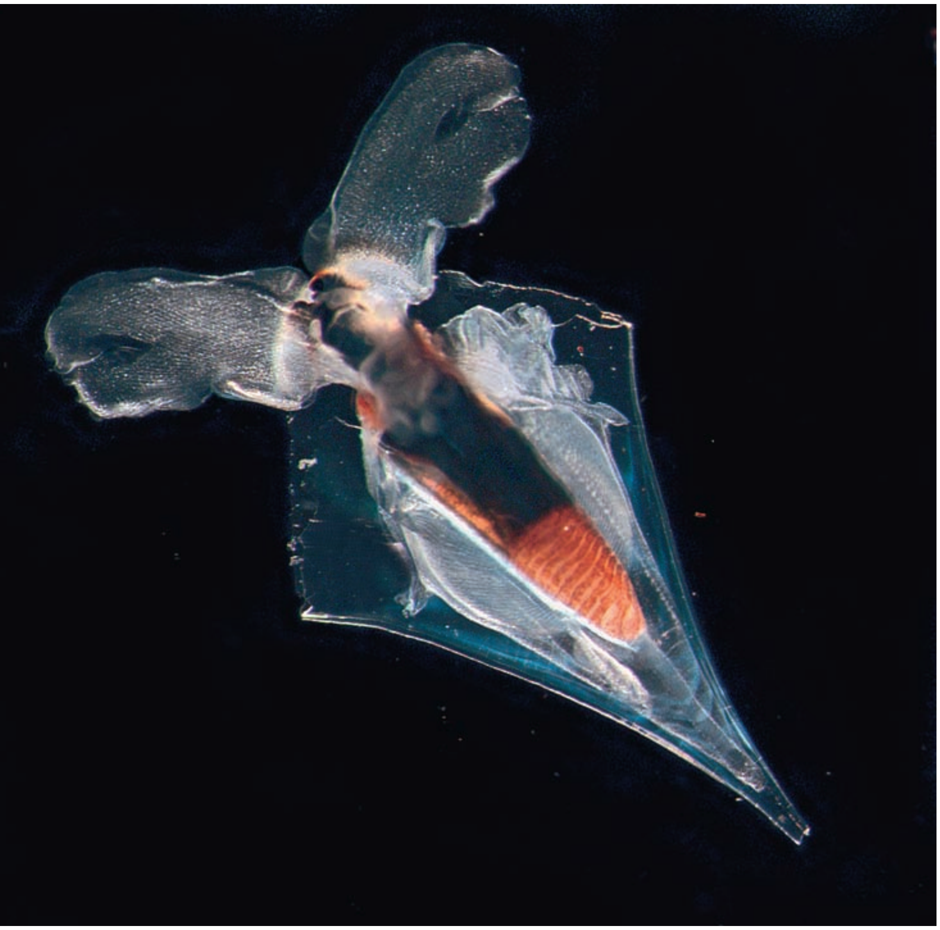


FIGURE 15.10 In pteropods, like this *Clio pyramidata*, the foot is typically expanded into "wings," which the animal uses to swim. Pteropods have a shell like most other molluscs, but it is greatly reduced.

the deep sea—release their eggs or young into the water column, and the larvae spend the early part of their lives in the plankton. Such temporary members of the plankton are called **meroplankton.** Coastal waters are particularly rich in meroplankton.

Invertebrates often have a particular type of larva that is characteristic of the group (Fig. 15.11). Some invertebrates have a whole series of different larval stages (see Fig. 7.39). Nearly all marine fishes also have planktonic larvae.

The meroplankton are the larval stages of invertebrates and fishes that spend only part of their lives in the zooplankton.

Small larvae tend to feed mostly on phytoplankton; larger ones eat zooplankton. If there is a series of stages, as in crustaceans, the larvae may feed on phytoplankton initially and later switch to zooplankton. Fish larvae, too, often change from herbivores to carnivores as they grow (see Fig. 15.24).

The Nekton

Plankton are by far the most abundant organisms in the sea, and they form the base of the epipelagic food chain. Most of us, however, are more familiar with the **nekton,** the large, strong swimmers. Fishes, marine mammals, and squids are the most abundant nekton. Turtles, sea snakes, and penguins are also included.

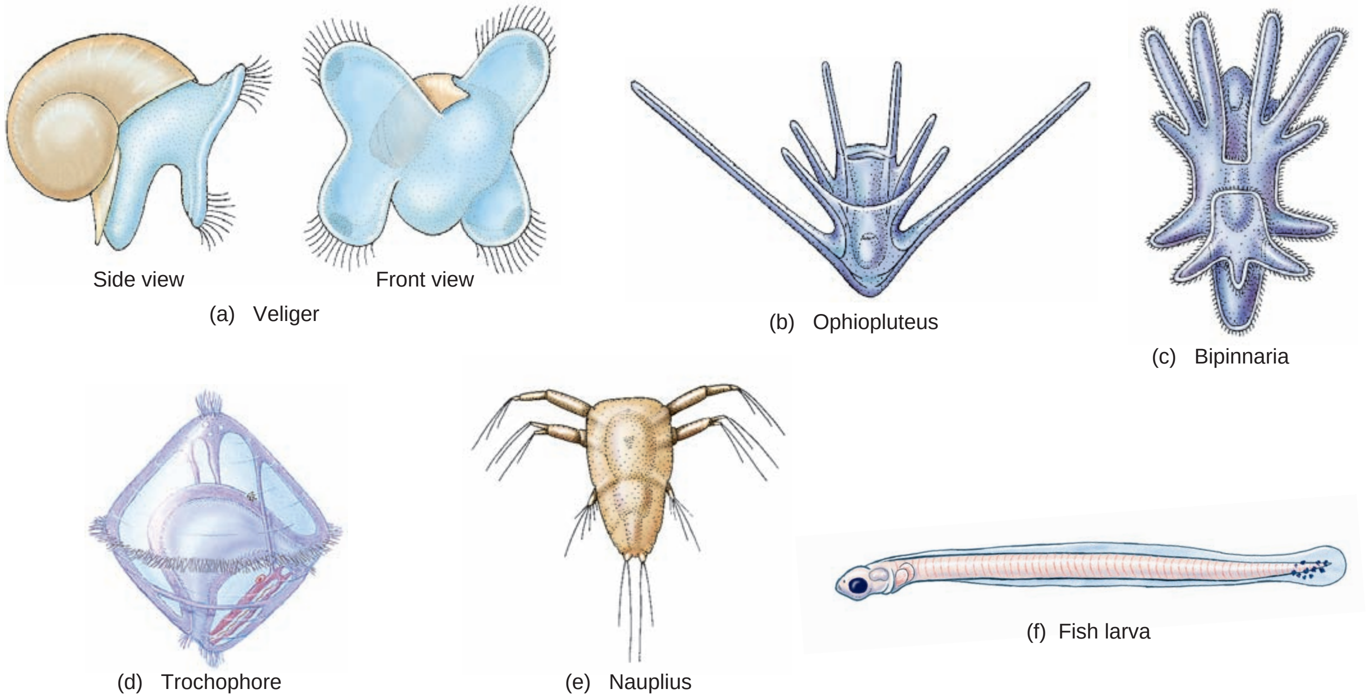


FIGURE 15.11 There is tremendous variety in the larvae found in the meroplankton. Some examples are (*a*) the veliger of molluscs, (*b*) the ophiopluteus of brittle stars, (*c*) the bipinnaria of sea stars, (*d*) the trochophore of polychaete worms and some molluscs, (*e*) the nauplius of many crustaceans, and (*f*) fish larvae.

Practically all nekton are carnivorous. **Planktivorous** nekton, those that eat plankton, include small fishes like herrings, sardines, and anchovies. They also include the world's largest fishes, the whale shark (*Rhiniodon typus*) and basking shark (*Cetorhinus maximus*). The largest nekton of all, baleen whales, also eat plankton, mostly krill. Seals, penguins, squids, and an assortment of fishes, including salmon, tunas, and flying fishes, also eat krill.

Fishes like lanternfishes that stay in deeper water during the day and swim up into the epipelagic at night (see "Vertical Migration and the Deep Scattering Layer," p. 364) consume large amounts of zooplankton. These fishes are important foods for some large epipelagic nekton, such as tunas and dolphins, that dive into deeper water to feed.

Most species of nekton, however, eat other nekton rather than plankton. Fishes, squids, and large crustaceans are the main foods. Epipelagic predators are usually not fussy and will eat many different prey, provided they are the right size. In general, the larger the predator, the larger the prey, though there are exceptions like baleen whales and whale sharks. Thus, small fishes like herrings have small prey: zooplankton. Bigger fishes eat these small fishes and in turn are eaten by even bigger predators. At the top of the food chain are the largest predators of all, the top predators, which eat the largest prey. The sperm whale (*Physeter catodon;* see Fig. 1.19), the largest of all nekton except baleen whales, eats giant squid more than 10 m (33 ft) long. There are other top predators that eat massive prey. Among predators, killer whales (*Orcinus orca*) are second in size only to the sperm whale. They not only eat porpoises and seals, but by hunting in groups can also attack and kill baleen whales. Large sharks such as the great white (*Carcharodon carcharias*) and makos (*Isurus*) eat seals, billfishes like marlins and sailfishes, and even other sharks.

Nearly all the epipelagic nekton are predators. A few eat plankton, but most species eat other, usually smaller, nekton.

LIVING IN THE EPIPELAGIC

Every environment places special demands on the organisms that live there, and the epipelagic is no exception. The adaptations of epipelagic organisms largely center around two main needs: the need to stay in the epipelagic and the need to eat and avoid being eaten.

Staying Afloat

To live in the epipelagic, organisms must *stay* in the epipelagic. Epipelagic organisms face a fundamental problem: Cells and tissue are denser than water. Shells and skeletons are even more dense. Thus, organisms sink unless they have some adaptation to prevent it. This is not a problem for organisms on the bottom, but organisms that live near the surface must avoid sinking to stay in their habitat.

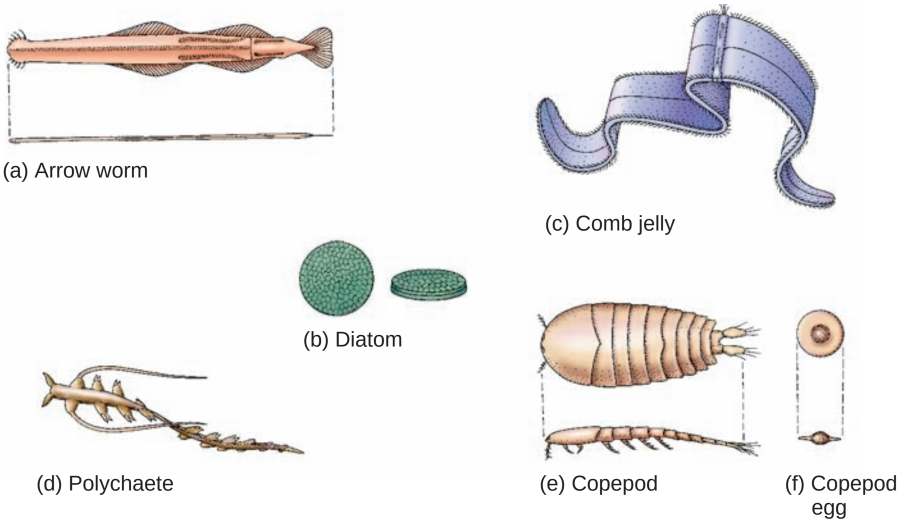
Phytoplankton have to stay in relatively shallow water to get enough light for photosynthesis. Once a phytoplankton cell sinks or is carried by water movement out of the photic zone it is doomed, unless it can somehow get back into the sunlit layer. Animals, too, whether zooplankton or nekton, must be able to stay near the surface, not because they need sunlight but because their food is found in the shallow waters.

Organisms that can't swim have two basic ways to keep themselves from sinking out of the epipelagic. One is to increase their water resistance so they sink slower. The other is to be more buoyant so they don't sink in the first place. Buoyancy also benefits organisms that swim because it allows them to stay at a given depth with less work. This applies not only to the nekton, which by definition are strong swimmers, but also to zooplankton and even some phytoplankton, like dinoflagellates. They swim up and down in the water column even though they can't swim strongly enough to resist the currents.

Organisms must avoid sinking to stay in the epipelagic. They do so by increasing water resistance and increasing buoyancy.

Increased Resistance How fast an organism of a given weight sinks depends on how much water resistance, or **drag,** it encounters. The drag depends on how much water a moving organism pushes in front of it and the amount of friction between the water and the organism's surface. For small organisms like most plankton, drag depends mostly on surface area: the higher the surface area, the higher the water resistance and the slower the organism sinks. This is one reason plankton are usually small: Small organisms have more surface area per unit volume than large organisms (see "Surface-to-Volume Ratio," p. 76) and thus a slower sinking rate.

An organism's shape can also increase its surface area to make it sink slower. The parachute-like shape of many jellyfishes helps slow sinking. Many plankton have extremely flat shapes (Fig. 15.12). You can see how this helps slow sinking with a simple experiment.


(a) Arrow worm

(b) Diatom

(c) Comb jelly

(d) Polychaete

(e) Copepod

(f) Copepod egg

FIGURE 15.12 Planktonic organisms with flat shapes include (*a*) some arrow worms (*Sagitta*), (*b*) many diatoms, (*c*) *Cestum,* a highly modified comb jelly, (*d*) *Tomopteris,* a planktonic polychaete worm, (*e*) certain copepods, such as *Sapphirina,* and (*f*) some copepod eggs.

Take two sheets of paper and crumple one into a ball. Drop both pieces from the same height. The flat sheet will take much longer to hit the ground because it offers more air resistance. Exactly the same principle applies in the water. A flat shape has another advantage for phytoplankton. Note how the flat sheet of paper zigzags from side to side as it falls. Flat phytoplankton cells do the same thing. The back-and-forth motion keeps seawater flowing over the cell's surface, renewing the layer of water with which the cell exchanges gases, nutrients, and waste products.

Long projections or spines are another common adaptation to increase surface area in planktonic organisms (Fig. 15.13). Spines have the added advantage of making the organism harder to eat. Many phytoplankton form chains, another adaptation that slows sinking. Chains sink slower than the individual cells would if the chain were broken up.

Swimming organisms rarely have spines or other features that increase surface area, since this would increase water resistance and make swimming harder. They usually have adaptations that *reduce* drag and make it easier to move through the water.

Increased Buoyancy The second way that epipelagic organisms stay near the surface is to be more buoyant. Unlike adaptations to resist sinking, buoyancy reduces the tendency to sink in the first place.

One common adaptation for buoyancy is to store **lipids,** such as oils or fats, in the body. Being less dense than water, lipids tend to float. Many plankton—notably diatoms, copepods, and fish eggs and larvae—contain oil droplets. Many adult epipelagic fishes also gain buoyancy by storing lipid. This is especially true of sharks, tunas and their relatives, and other species in which the swim bladder is poorly developed or missing altogether. Epipelagic sharks, for example, have enlarged livers with a very high oil content. Whales, seals, and other marine mammals have a great deal of buoyant fat in a thick layer of blubber under the skin (see Fig. 4.2).

Oils and fats also serve other functions. Lipids are the most efficient way to store energy, for instance. In marine mammals the blubber provides insulation from the cold as well as buoyancy. Insulation is especially important to warm-blooded animals, which must burn energy to maintain their body temperatures (see "Temperature," p. 75).

Pockets of gas are another adaptation for buoyancy. Cyanobacteria, for example, have tiny gas bubbles, or vacuoles, inside their cells. They are able to change the number and buoyancy of the vacuoles. This allows them to increase buoyancy to move up in the water column or decrease it to sink. Some other plankton, especially large ones, have special gas-filled floats. Such floats are especially common in organisms that live right at the sea surface, as described in the next section. Similarly, most epipelagic bony fishes have **swim bladders** for buoyancy.

A gas-filled bladder or float provides much more buoyancy than, for example, lipid, but it has a major disadvantage. Gas expands and contracts as the animal moves up and down in the water column and the pressure changes. When the volume of gas changes, so does the amount of buoyancy. To control its buoyancy, a fish must be able to regulate the amount of gas in its swim bladder. Most fishes can do this, but the actual mechanism varies. Some fishes pump gas in and out of the bladder through a special duct. They can adjust fairly rapidly to changes in pressure. Other fishes regulate the amount of gas in their swim bladders much more slowly and cannot cope well with depth changes. Many fishers have pulled up fish with bulging eyes or the stomach protruding from the mouth (see Fig. 3.15). This happens when the gas in the swim bladder expands as the fish is brought to the surface. In normal life the fish would never come to the surface or would surface much more slowly than it did on the end of the line.

The swim bladder is often poorly developed or absent in active fishes that frequently change depth, such as tunas. It never evolved in sharks. Such fishes must compensate for the loss of buoyancy. In addition to their large oily livers, sharks have large, stiff fins and asymmetrical tails that provide lift when the shark swims (see Fig. 8.12). Members of the tuna family also rely on stiff, almost wing-like fins and constant swimming to provide lift.

Yet another way to gain buoyancy is to control the composition of the body fluids. By excluding heavy ions, like sulfate (SO_4^{-2}) and magnesium (Mg^{+2}), and replacing them with lighter ones, especially ammonium (NH_4^+) and chloride (Cl^-), organisms can reduce their density and become more buoyant. Certain dinoflagellates are known to do this, and there is evidence that other phytoplankton do too. So do various zooplankton, including salps, comb jellies, and some squids.

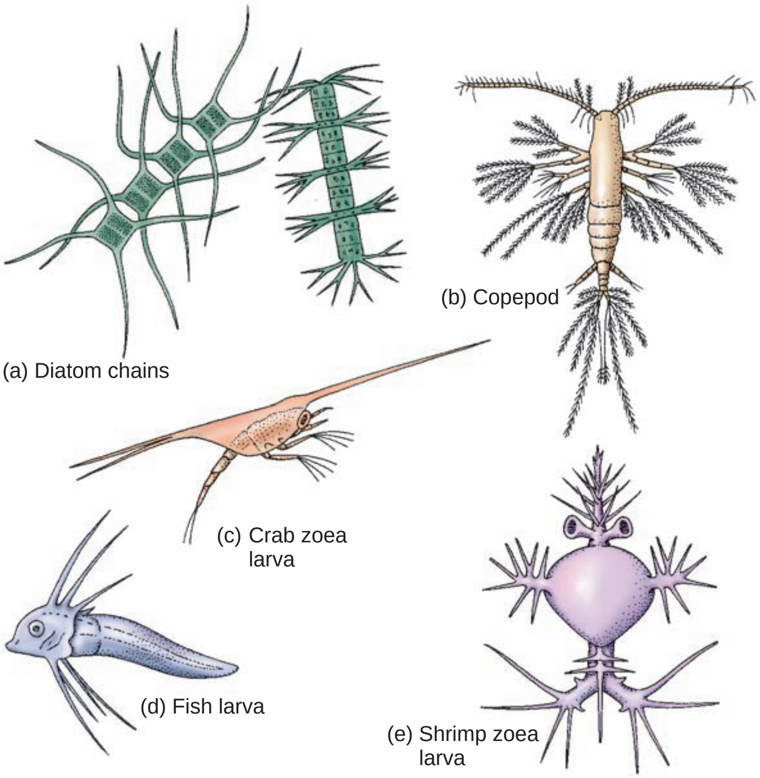


FIGURE 15.13 Some planktonic organisms have long spines or projections. They may also form chains. Examples are (*a*) diatoms, (*b*) copepods like *Augaptilus,* (*c*) zoea larvae of porcellanid crabs, (*d*) fish larvae (*Lophius*), and (*e*) zoea larvae of *Sergestes,* a shrimp.

Mechanisms that increase the buoyancy of epipelagic organisms include the storage of lipids, gas-filled floats, and the substitution of light ions for heavy ones in internal fluids.

The Floaters The plankton include an unusual and highly specialized group of organisms that live at the very surface of the ocean. Organisms that live right at the sea surface but remain underwater are known as **neuston,** and those whose bodies project through the sea surface into the air are called **pleuston.**

All plankton need to keep from sinking, but the neuston and pleuston have to go one step further and actually float. The most common method of doing this is to have some sort of gas-filled structure to provide buoyancy. There are many variations on this seemingly simple theme.

The upper surface of the by-the-wind sailor (*Velella*), a colonial, jellyfish-like cnidarian, is specialized as a float (Fig. 15.14). The float protrudes into the air and acts like a sail, pushing the colony along in the wind. The Portuguese man-of-war (*Physalia*), a siphonophore, is famous for its powerful sting (see "The Case of the Killer Cnidarians," p. 122). Like the by-the-wind sailor, part of the colony acts as a sail (Fig. 15.15). Several other cnidarians live at the sea surface. Some can even control the buoyancy of their floats and sink below the surface for shelter during storms.

Despite their powerful stinging cells, these relatives of jellyfishes have enemies. The violet shell (*Janthina*) makes a raft of mucus filled with bubbles from which it hangs upside down. These inch-long snails drift about, eating Portuguese men-of-war and other delicacies when they find them. Another mollusc, a sea slug (nudibranch) called *Glaucus,* stays afloat by swallowing a bubble of air. It feeds on the by-the-wind sailor and its relative, the small, disk-shaped *Porpita* (Fig. 15.16). *Porpita*'s stinging cells, still capable of firing, end up in the flaps that protrude from the sea slug's back and will sting animals that disturb it. Thus, *Porpita* provides not only food but also protection for the sea slug.

One unusual inhabitant of the surface doesn't have a float. In fact, it doesn't actually float at all. The water strider (*Halobates*), the only insect that lives in the open ocean, skims over the water surface (Fig. 15.17). It is closely related to the water striders common in lakes and ponds. The water strider isn't marine in the strict sense because it cannot swim and drowns if it falls through the surface. Still, it manages to live all over the oceans.

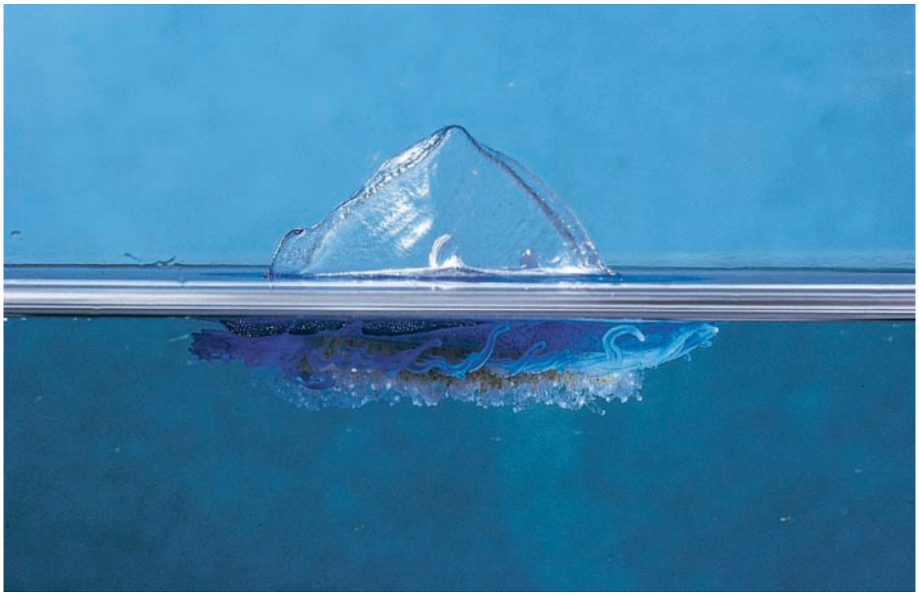


FIGURE 15.14 The by-the-wind sailor (*Velella*).

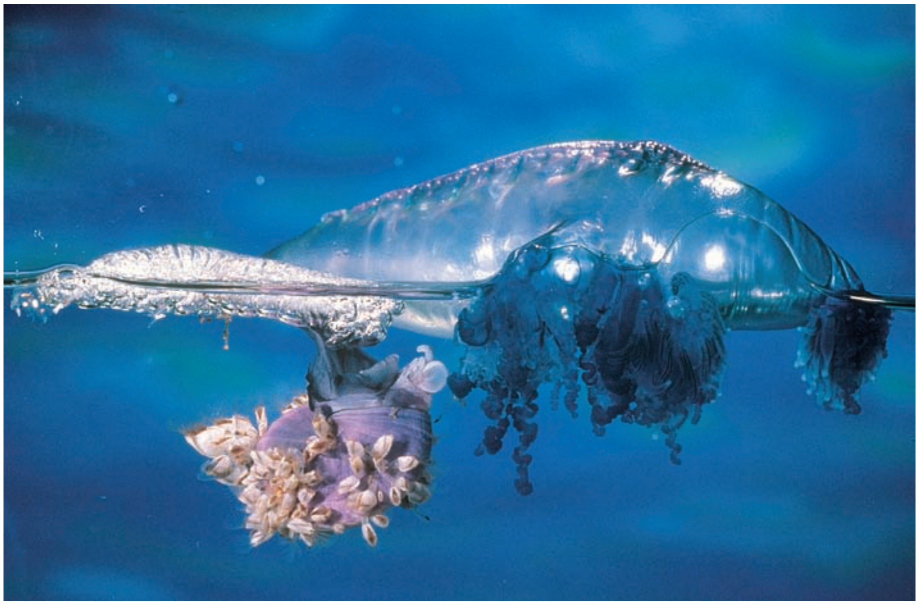


FIGURE 15.15 A violet snail (*Janthina janthina;* left), covered with gooseneck barnacles, eats a Portuguese man-of-war (*Physalia physalis;* right).

Predators and Their Prey

Many of the adaptations of epipelagic animals, or for that matter any animals, are related to the need to find food and at the same time avoid being eaten.

Sense Organs Predators and their prey play a continual game of hide-and-seek. The predator tries to find its prey and attack before the victim can escape, while the prey wants as much warning of approaching enemies as possible. Most animals in the epipelagic therefore have highly developed sense organs to help them detect their prey and enemies.

The epipelagic has plenty of light to see by, at least during the day, so it is no surprise that vision is important to many epipelagic animals. Many zooplankton have well-developed eyes. Most can't see actual images, but they can detect motion, shapes,

Swim Bladder A gas-filled sac that lies inside the body cavity of most bony fishes.
- Chapter 8, p. 157; Figure 8.12

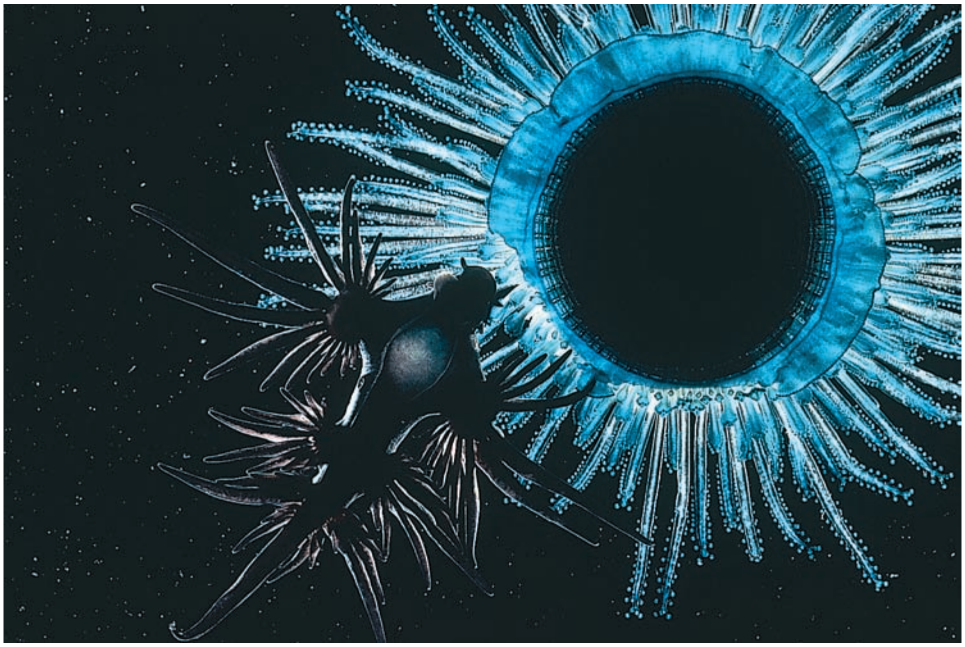


FIGURE 15.16 The pelagic sea slug (*Glaucus*) feeding on *Porpita,* a relative of jellyfishes. The sea slug not only gets a meal but also uses *Porpita's* stinging cells for defense.

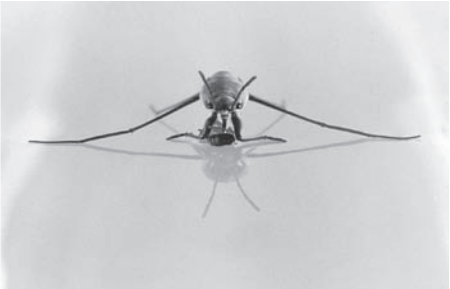


FIGURE 15.17 The marine water strider (*Halobates sericeus*) relies on greatly elongated legs and the water's surface tension to skate on the surface.

and shadows. Copepods and other zooplankton probably use vision to locate their prey and avoid predators.

Squids, fishes, and marine mammals all have good eyesight. Vision is especially important to nekton in the epipelagic because there are no solid structures that can be used for concealment. In other environments, animals can hide in the sediments, under rocks, or behind seaweeds. There are no such hiding places in the epipelagic. The large, well-developed eyes of most epipelagic fishes (Fig. 15.18) and other nekton are used not only to find prey and watch for predators, but also to find mates and stay together in schools (see "Schooling," p. 167).

Fishes have another remote sensing system: the **lateral line.** Like all fishes, those in the epipelagic are extremely sensitive to vibrations in the water. Fishes use their lateral lines to stay in touch with schoolmates and to detect predators. Even blind fishes can school and react to the lunge of an enemy. Most predatory fishes—including sharks, tunas, and billfishes—also have well-developed hearing and are strongly attracted to splashes on the surface and irregular vibrations in the water, the kinds of vibrations made by an injured fish. Another remote sensing system, **echolocation,** is found in dolphins and some other cetaceans. This sophisticated built-in sonar allows them to locate their prey at a distance (see "Echolocation," p. 200).

> Epipelagic animals have well-developed sense organs, especially vision, the lateral lines and hearing of fishes, and echolocation in cetaceans.

Coloration and Camouflage Just because there are no hiding places doesn't mean that epipelagic organisms cannot conceal themselves. Indeed, **protective coloration,** or camouflage, is nearly universal among epipelagic animals. This isn't surprising in a world where the hunters rely so heavily on vision to find their victims, and the prey use vision to get away.

One way to be inconspicuous in the vast, watery world of the epipelagic is to be transparent. This adaptation is seen in a variety of zooplankton, some of which are almost perfectly clear (Fig. 15.19). Gelatinous zooplankton like some jellyfishes, salps, larvaceans, and comb jellies are probably the best at being invisible. Many other groups of zooplankton are at least partially transparent, with perhaps only the eyes, a few spots of pigment, or the internal organs visible. Some nearly transparent zooplankton have a faint, bluish tinge, possibly helping them blend in with the surroundings.

Another common form of protective coloration, particularly in nekton, is **countershading,** where the back (dorsal surface) is dark, usually green, blue, or black, and the belly (ventral surface) is white or silver. Countershading is particularly well suited to the epipelagic. To a predator looking down, the ocean depths are a dark blue. Viewed from above, the dark back of a countershaded fish blends in against the dark background. Looking up, on the other hand, the predator sees the bright light filtering down from above and the silvery-white sea surface. Against this bright background a dark object stands out like a sore thumb, but the silvery-white undersides of epipelagic nekton reflect light and match the bright surface. Laterally compressed bodies, also common, reduce the size of the silhouette, whether viewed from above or below (Fig. 15.20).

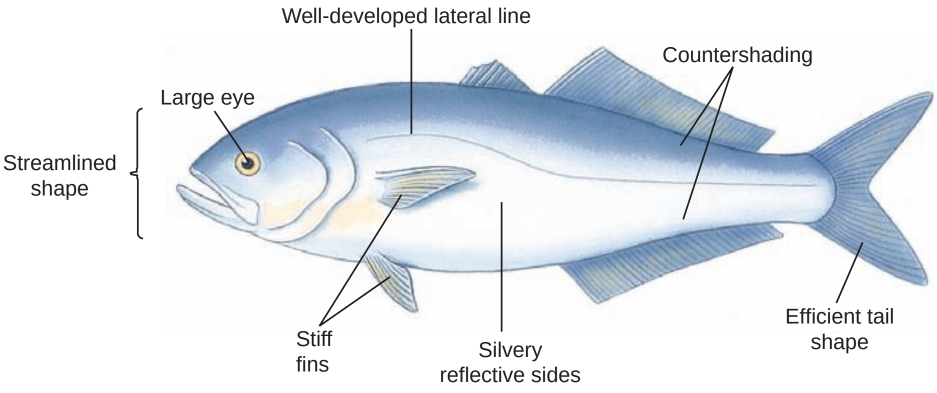


FIGURE 15.18 Typical adaptations of epipelagic fishes.

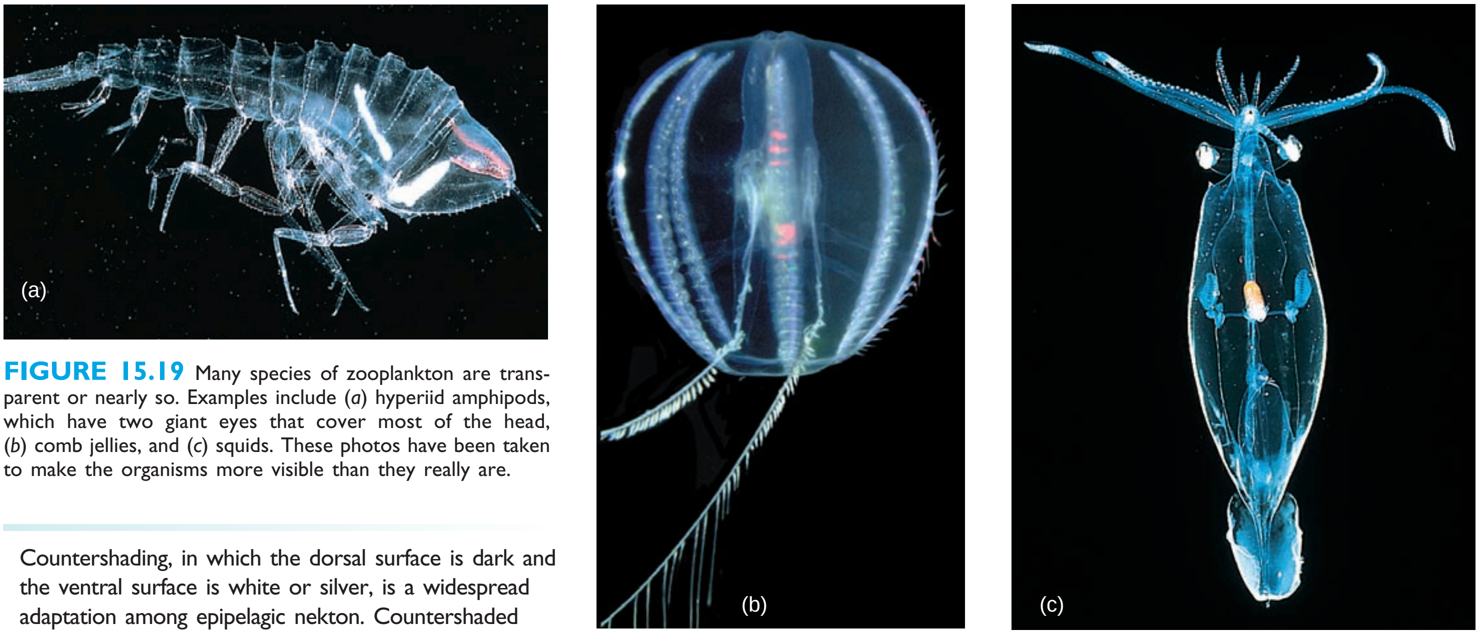


FIGURE 15.19 Many species of zooplankton are transparent or nearly so. Examples include (*a*) hyperiid amphipods, which have two giant eyes that cover most of the head, (*b*) comb jellies, and (*c*) squids. These photos have been taken to make the organisms more visible than they really are.

Countershading, in which the dorsal surface is dark and the ventral surface is white or silver, is a widespread adaptation among epipelagic nekton. Countershaded organisms blend in against the background whether they are viewed from above or below.

Most epipelagic fishes have silvery sides that reflect light. This helps them blend in when viewed from the side as well as from above or below. It is also common for them to have vertical bars or irregular patterns that help break up their outline in the dappled underwater light.

Flying fishes (*Cypselurus*) have evolved a distinctive defense that is not exactly camouflage but does make them hard to see, at least temporarily. When threatened, flying fishes burst out of the water and glide through the air on their greatly enlarged pectoral fins (Fig. 15.21). To a predator, the flying fish seems to have disappeared, because it is difficult to see past the surface into the air. This strategy is only partly effective, however, and flying fishes are a favorite food of many epipelagic predators.

Swimming: The Need for Speed Protective coloration or not, the keen senses of epipelagic predators enable them to find their prey. When this happens the prey's only hope is to flee, because there are no hiding places. Whether the prey gets away or the predator gets a meal depends on which swims faster. The emphasis is on sheer speed, as opposed to maneuverability, or being able to burrow in the bottom or hide in crevices in the rocks. It is no coincidence that the epipelagic contains the world's most powerful swimmers (see "Swimming Machines," p. 345).

While plankton often have adaptations to increase drag in order to slow their sinking, nekton, who must work to move through the water, have adaptations to *reduce* drag. Practically all epipelagic nekton have streamlined bodies that make swimming easier and more efficient (see Fig. 9.14). They rarely have bulging eyes, long spines, or other projections that increase resistance. Instead, their bodies are sleek and compact. They often have smooth body surfaces to help them slide through the water. Epipelagic fishes usually have small scales, or none at all, and dolphins and whales have lost nearly all their hair. Fishes produce mucus that actually lubricates the body surface, allowing them to slip through the water even more easily.

Lateral Line A system of canals on the head and sides of fishes that helps them detect vibrations in the water.

- Chapter 8, p. 165; Figure 8.19

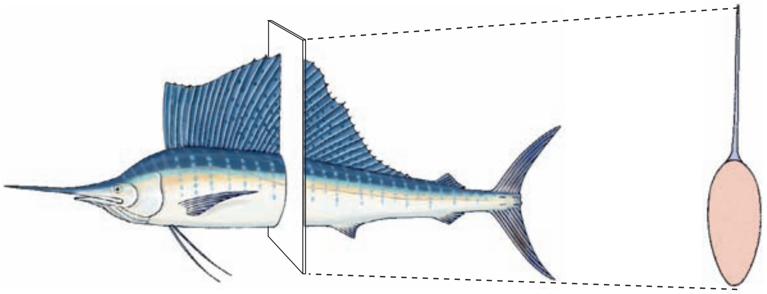


FIGURE 15.20 Like many epipelagic fishes, the sailfish (*Istiophorus platypterus*) has a laterally compressed body; that is, it is high and narrow when viewed in cross section.

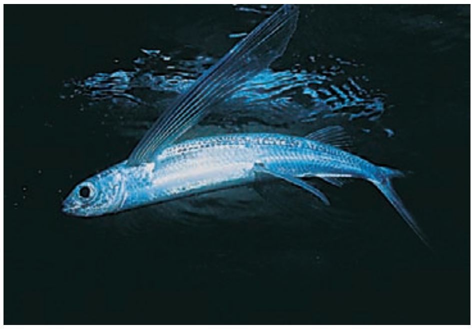


FIGURE 15.21 Flying fishes (*Cypselurus*) can't actually fly, but their expanded pectoral fins allow them to glide for long distances.

Epipelagic nekton are also firm and muscular, another adaptation for swimming. The force produced by these muscles is delivered almost entirely by the tail. Epipelagic fishes rarely swim with their pectoral fins, which are used only for steering and lift. Most epipelagic fishes have a tail that is high and narrow. Studies have shown this to be the most efficient shape for high-speed swimming. Tunas and sharks have also independently evolved specialized long tendons, not found in other fishes, that efficiently transfer the muscles' power back to the tail.

Bony fishes in other habitats typically have fins with movable spines connected by a thin membrane, making them dexterous and flexible. By contrast, the fins of epipelagic bony fishes tend to be stiff, giving them the strength to provide maneuverability and lift at high speed. These stiff fins aren't much good for hovering, swimming backward, poking into holes and crevices, or other activities that require tight maneuvers at slow speed. Epipelagic fishes don't do such things often, anyway.

Epipelagic nekton not only have a lot of muscle, but their muscles are strong and efficient. Fishes have two kinds of muscle, red and white—the equivalent of the light and dark meat on a turkey. Red muscle gets its color from a high concentration of **myoglobin** and can store a lot of oxygen. It is best suited for long, sustained effort. White muscle, on the other hand, provides short bursts of power. Epipelagic fishes use their red muscle for sustained cruising, and typically have more red muscle than coastal fishes, which don't usually do as much sustained swimming. Epipelagic fishes still have white muscle that kicks in when they need an extra burst of speed.

Typical epipelagic nekton have sharp eyesight, countershading, streamlined bodies, well-developed and efficient muscles, and high, relatively narrow tails.

Muscle works more efficiently at warm temperatures. Epipelagic sharks, tunas, and billfishes have evolved a system to conserve the heat generated by their muscles and keep their internal temperature above that of the surrounding water. These fishes can almost be considered "warm-blooded." In most fishes, heat generated in the muscles is carried by the blood to the skin and then lost to the water. "Warm-blooded" fishes have a special arrangement of the blood vessels known as the **rete mirabile,** or "wonderful net." In this arrangement (Fig. 15.22), body heat carried outward in the blood is transferred to inward-flowing blood and taken back into the body. This greatly reduces heat loss. The fish's core temperature remains well above that of the surrounding water, while the skin has nearly the same temperature as the water.

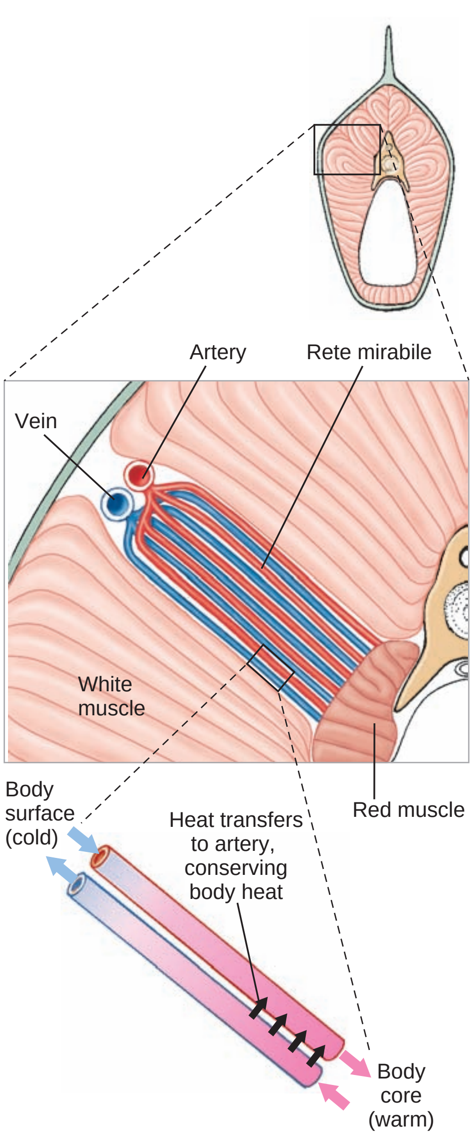


FIGURE 15.22 In "warm-blooded" epipelagic fishes, small veins and arteries are arranged in such a way that heat generated by muscular activity at the body core is carried back to the core in returning blood. The veins and arteries are packed into a complex network known as the rete mirabile, or "wonderful net."

Vertical Migration The surface layers of the ocean contain by far the most food in the pelagic realm. They can be a dangerous place, however, with voracious predators zooming around and nowhere to hide. Some zooplankton spend only part of their time near the surface and retreat to safer territory when not feeding. These animals undertake **vertical migration.** During the day they live at considerable depth, usually at least 200 m (650 ft) or so (Fig. 15.23). At these depths there is not much light, so the zooplankton are relatively safe from predators that use vision. At night, the zooplankton swim up to the surface layers to feed on phytoplankton and other zooplankton. Experiments in deep tanks have shown that zooplankton vertically migrate only if predatory fish are in the tank; they stop migrating when the predators are removed.

Vertically migrating zooplankton stay below the photic zone during the day. At night they migrate to the surface to feed.

These daily movements require a lot of energy. For an organism that is 2 mm long, a 200-m migration is the rough equivalent of a 200-km (120-mi) swim for a human! That is a long way to go to avoid predators when many other zooplankton withstand predation without migrating. Various explanations for vertical migrations in addition to escaping predation have been proposed. Zooplankton may be able to slow their metabolism and conserve energy by spending part of their time in the deep water, which is cold and reduces their body temperature. This is somewhat like sleep or hibernation. It has also been suggested that zooplankton migrate to avoid toxins produced by some phytoplankton. The phytoplankton produce more toxins during the day, when they are actively photosynthesizing.

Many species of nekton, mainly fishes and some large shrimps, also make vertical migrations. These animals generally migrate to much greater depths than zooplankton (see "Vertical Migration and the Deep Scattering Layer," p. 364).

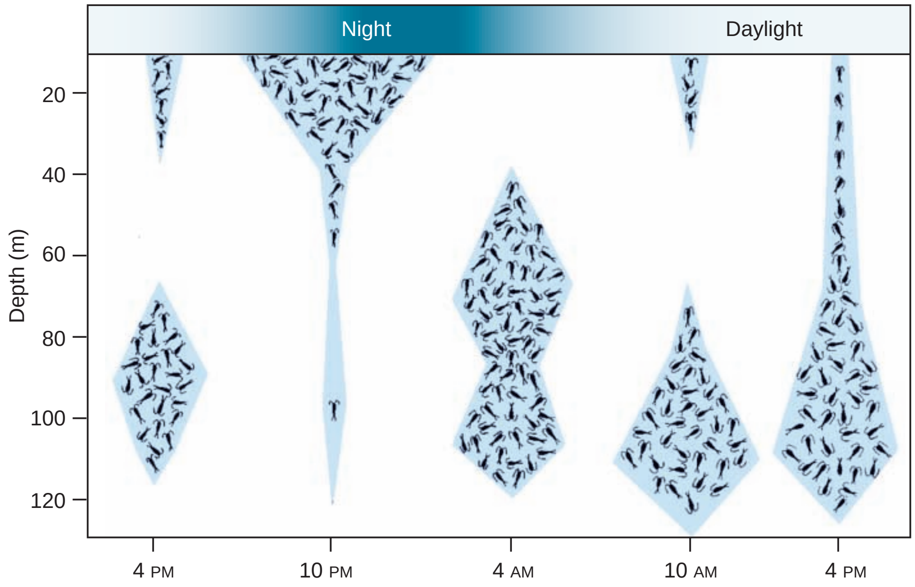


FIGURE 15.23 The depth distribution at different times of day of a vertically migrating copepod.

EPIPELAGIC FOOD WEBS

Epipelagic food webs are of great interest, especially because epipelagic fisheries provide food and employment to millions (see "Food from the Sea," p. 380). Species that are caught commercially can be understood and managed only if we understand the rest of the food web on which they depend.

Trophic Levels and Energy Flow

The trophic structure of the epipelagic is extremely complex. The feeding habits of most epipelagic species are poorly known, if at all. It's hard to describe the trophic structure of a community if you don't even know what many of the animals eat!

Another difficulty in understanding epipelagic food webs is that most of the animals eat a variety of prey, often from different trophic levels. Zooplankton such as copepods often eat both phytoplankton and zooplankton; thus, they function as both herbivores and carnivores. Nekton, too, consume prey at different levels on the food web. A tuna, for example, may act as a secondary consumer when it eats krill, as a third-level consumer when it eats a sardine that ate zooplankton, and as a fourth-level consumer when it eats a mackerel that ate a flying fish that ate zooplankton. This makes it difficult to assign many animals to a particular trophic level.

Yet another complication is that most epipelagic animals consume different prey at different times in their lives. Most eat different food as larvae than they eat as adults, and even the larvae often switch from phytoplankton to zooplankton. Even after they leave the larval stage, many fishes eat different prey as they grow larger (Fig. 15.24).

The basic flow of energy in the epipelagic can be depicted as phytoplankton → zooplankton → small nekton → large nekton → top predators. The top predators, of course, are also nekton. This scheme is greatly simplified, and each level contains a mini-web. Within the zooplankton, for example, there are herbivores and several levels of carnivores, forming a food web among themselves. There is also an important side branch called the microbial loop, which is described in the next section.

Epipelagic food chains usually have many steps and are generally longer than in other ecosystems. The number of steps varies: Tropical food webs tend to have more levels than those in colder waters. Even in cold waters there may be five or six steps between the primary producers in the phytoplankton and a top predator. There are exceptions, of course. The diatoms-to-krill-to-whales chain (see Fig. 10.13), for example, is among the shortest of food chains.

The epipelagic is an exception to the rule of thumb that only about 10% of the energy contained in one trophic level is passed on to the next (see "The Trophic Pyramid," p. 223). Epipelagic herbivores convert more than 20%, on average, of the energy derived from phytoplankton into growth. Epipelagic carnivores, too, are more than 10% efficient, though not as efficient as the herbivores.

Even with their high efficiency, the length of epipelagic food webs means that most of the energy fixed by phytoplankton is lost before it reaches the top carnivores. After all, even an efficiency of 20% means that 80% of the energy is lost in just one step. Large animals that feed directly on plankton have an advantage in that they have more food available than do predators that eat other high-level carnivores. By feeding directly at low trophic levels, they eliminate many intermediate steps. It is no accident that the largest epipelagic nekton, baleen whales and whale sharks, and the most abundant epipelagic fishes, like anchovies and herrings, eat plankton.

Epipelagic food chains tend to be long and complex. The transfer of energy between trophic levels is more efficient than in many other ecosystems, but because there are often many levels not much of the energy fixed in primary production reaches the top of the food chain.

Until a few years ago, most of the primary production in the epipelagic was thought to flow through the simplified food chain of phytoplankton → zooplankton → nekton. "Phytoplankton" and "zooplankton" referred to the relatively large net plankton. The discovery of vast numbers of picoplankton and nanoplankton in the ocean greatly changed our understanding of epipelagic food webs.

The ocean contains huge amounts of **dissolved organic matter (DOM),** organic material that exists not as particles but in dissolved form. Some of the DOM simply leaks out of phytoplankton cells. Zooplankton spill a lot of DOM when they eat, and excrete it as waste. The largest source of DOM, however, results from the activities of viruses (see "Viruses," p. 86). There

Myoglobin A red muscle protein in vertebrates that stores oxygen.
• Chapter 8, p. 164

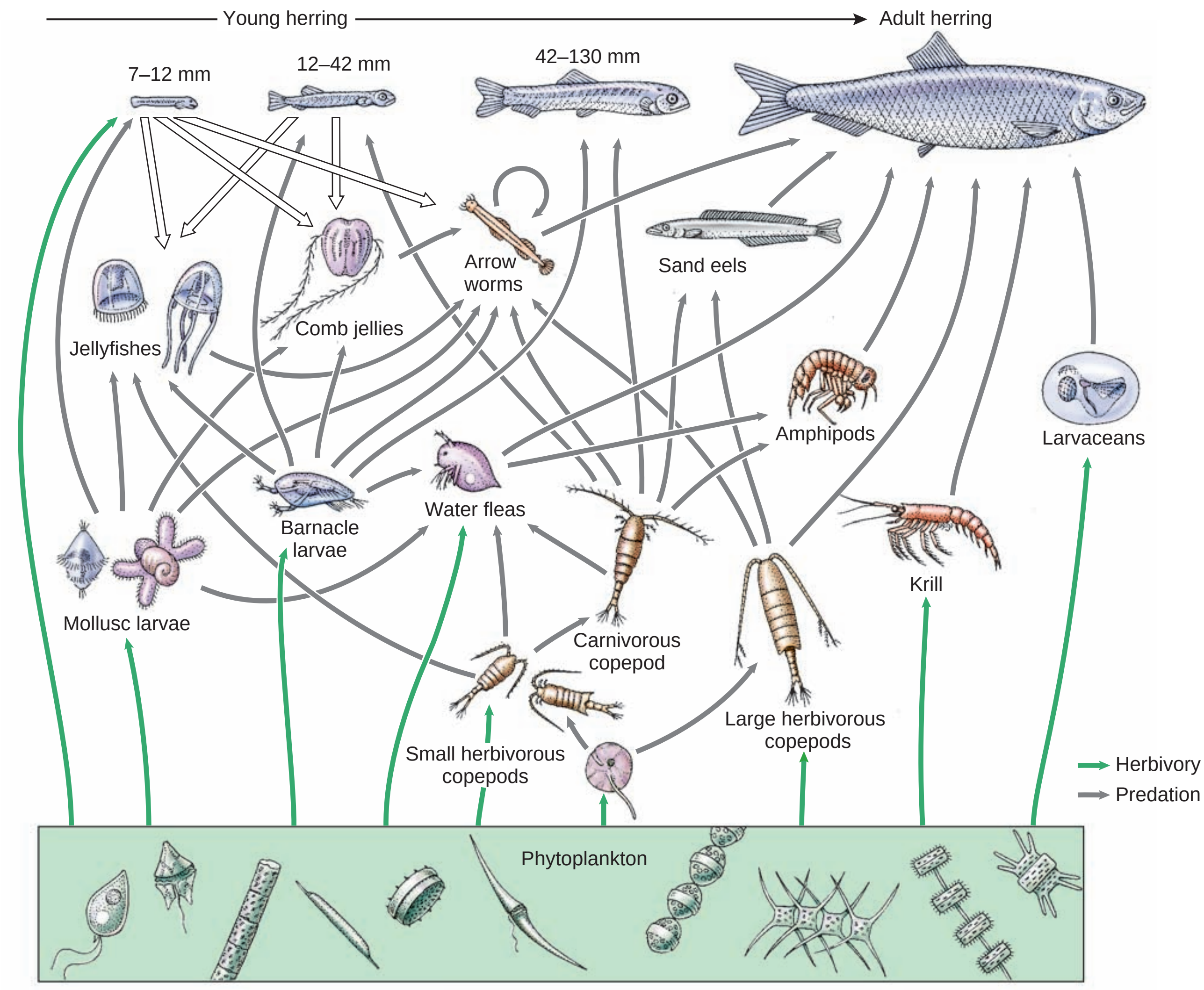

Young herring
Adult herring
7–12 mm
12–42 mm
42–130 mm
Arrow worms
Sand eels
Jellyfishes
Comb jellies
Amphipods
Larvaceans
Water fleas
Barnacle larvae
Mollusc larvae
Carnivorous copepod
Krill
Large herbivorous copepods
Small herbivorous copepods
Herbivory
Predation
Phytoplankton

FIGURE 15.24 The North Sea herring (*Clupea harengus*) eats different foods at different stages of its life. Its larval stages are eaten by predators that do not feed on adult herring (open arrows). Many, if not most, epipelagic animals have similarly complex feeding relationships. Illustrations of food webs are usually greatly simplified and gloss over such complexities. For example, how would this partial food web fit into the scheme shown in Figure 15.4?

are tens of millions of viruses per milliliter in the ocean that infect large numbers of organisms, particularly microbes. The viruses cause the infected cells to burst, releasing the cells' contents.

We may not think of such material as food in the ordinary sense, but it contains a lot of energy. Calorie counters who like sugar in their coffee are familiar with this fact. Very few animals, however, are able to use DOM as an energy source. Though some phytoplankton may be able to use it, it was once thought that the huge pool of energy in DOM went largely unused.

The Microbial Loop

We now know that the DOM in the ocean isn't just sitting there, but is part of a major energy pathway called the **microbial loop** (Fig. 15.25). The microbial loop starts with phytoplankton of all sizes. As much as *half* the organic matter manufactured by these primary producers becomes DOM. The DOM is not lost to the food web, but is used by bacteria and probably archaea. These microbes are so small that most animals can't eat them either, but they are eaten by tiny protozoans in the nanoplankton. The energy from DOM is finally passed up the rest of the food chain when net zooplankton eat the protozoans.

The "microbial loop," in simplified form, refers to the flow of energy through the series phytoplankton → DOM → bacteria → protozoans → zooplankton. Without the microbial loop, the energy in DOM would largely go unused. As much as half the primary production in the epipelagic is channeled through the microbial loop.

Another important role of protozoan grazers is in channeling the production of primary producers in the nanoplankton up the food chain. Again, these nanoplankton are too small for most zooplankton to eat.

Detritus—particulate rather than dissolved organic matter—is also important in the epipelagic, as in other marine food webs. Two important sources of detritus have already been

Swimming Machines

Tunas, mackerels, and billfishes swim continuously. Feeding, courtship, reproduction, and even "rest" are carried out in constant motion. As a result, practically every aspect of the body form and function of these swimming machines is adapted to enhance swimming ability.

The swimming feats of tunas and billfishes are amazing. They routinely cover vast distances in their annual migrations. One northern bluefin tuna (*Thunnus thynnus*) tagged southeast of Japan was recaptured off the Pacific coast of Baja California, Mexico, 10,800 km (6,700 mi) away. Most other tunas and billfishes also make long-distance migrations.

These long journeys are made in an impressively short time. Tagged northern bluefin have crossed the Atlantic in 119 days, averaging a straight-line distance of over 65 km (40 mi) per day. The fish actually cover a much greater distance because they constantly change direction, dashing here and there in search of food. Some tunas could cross the Atlantic in less than two months at their *slowest* cruising speed if they took a direct route.

Tunas and billfishes are primarily endurance swimmers, adapted for sustained cruising, but they are also accomplished sprinters and can make blistering, high-speed bursts. The fastest fish of all is the Indo-Pacific sailfish (*Istiophorus platypterus;* see Fig. 1.16), which can exceed 110 km/hr (70 mph) for short periods. No other fish can match this, but most tunas and billfishes are fast swimmers. Several large species can reach 75 km/hr (50 mph); some smaller ones are just as fast for their size. Most are so fast that they can easily outdistance their prey. Their phenomenal speed has probably evolved not so much to catch prey—they could do that at slower speeds—as to compete with schoolmates. The first one to the prey, after all, gets the meal.

Many adaptations of these fishes reduce water resistance. Interestingly, several of these hydrodynamic adaptations resemble features designed to improve the aerodynamics of high-speed aircraft. Though human engineers are new to the game, tunas and their relatives evolved their "high-tech" designs long ago.

Tunas, mackerels, and billfishes have made streamlining an art form. Their bodies are sleek and compact. The body shapes of tunas, in fact, are nearly ideal from an engineering point of view. Most species lack scales over most of the body, making it smooth and slippery. The eyes lie flush with the body and don't protrude. They are also covered with a slick, transparent lid that reduces drag. The fins are stiff, smooth, and narrow, also cutting drag. When not in use, the fins tuck into special grooves or depressions so they lie flush with the body and don't break up its smooth contours. Airplanes retract their landing gear in flight for the same reason.

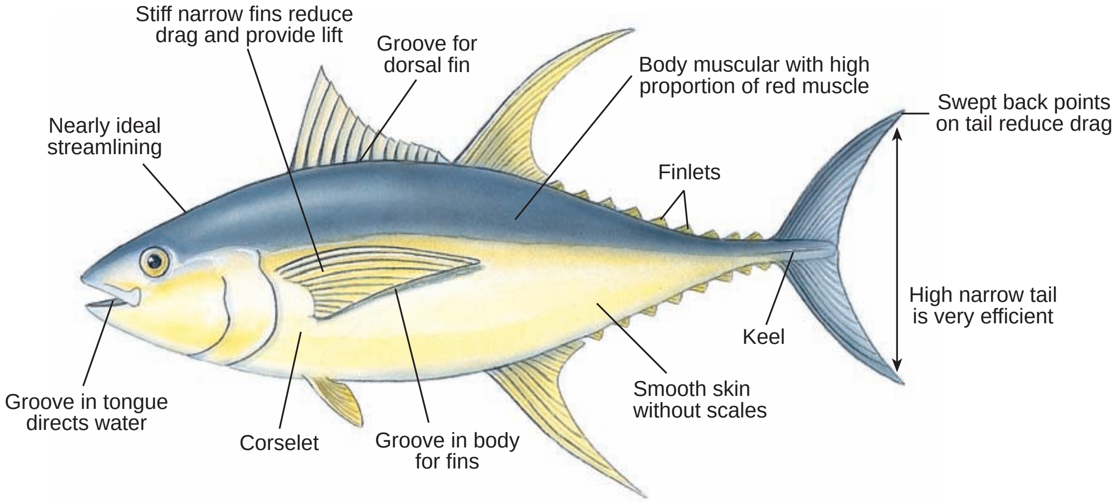
These fishes have even more complex adaptations to improve their hydrodynamics. The long bill of marlins, sailfishes, and swordfish (*Xiphias gladius*) probably helps them slip through the water. Many supersonic aircraft have a similar needle at the nose. Most tunas and billfishes have a series of keels and finlets near the tail. Although most of their scales have been lost, tunas and mackerels retain a patch of coarse scales near the head called the corselet. The keels, finlets, and corselet help direct the flow of water over the body surface in such a way as to reduce resistance. Again, supersonic jets have similar features.

Because they are always swimming, tunas can force water over their gills by simply opening their mouth. Accordingly, they have lost most of the muscles that other fishes use to suck water in and push it past the gills. In fact, tunas must swim to breathe. They must also keep swimming to avoid sinking, since most have largely or completely lost the swim bladder.

A potential problem is that opening the mouth to breathe detracts from the streamlining of these fishes and tends to slow them down. Some tunas have specialized grooves in their tongue. The grooves help channel water through the mouth and out the gill slits to reduce water resistance.

Tunas and billfishes have adaptations to increase forward thrust as well as to reduce drag. Again, they are the envy of engineers. Their high, narrow tails with swept-back tips are almost perfectly adapted for propulsion with the least possible effort. Perhaps most important of all to these and other fast swimmers is their ability to sense and make use of swirls and eddies in the water. They can slide past eddies that would slow them down and then gain thrust by "pushing off" the eddies. The race car driver who "slipstreams" and then "slingshots" past a leading car uses much the same principles, but not nearly as well. Scientists and engineers are beginning to study this ability of fishes in the hope of designing more efficient propulsion systems for ships.

The muscles of these fishes and the mechanism that maintains a warm body temperature are also highly efficient. A bluefin tuna in water of 7°C (45°F) can maintain a core temperature of over 25°C (77°F). This warm body temperature may help not only the muscles but also the brain and eyes work better. Billfishes have gone one step further. They have evolved special "heaters" of modified muscle tissue that warm the eyes and brain, maintaining peak performance of these critical organs. (See "Vision in Billfishes," p. 166).


Stiff narrow fins reduce drag and provide lift
Groove for dorsal fin
Body muscular with high proportion of red muscle
Swept back points on tail reduce drag
Nearly ideal streamlining
Finlets
High narrow tail is very efficient
Keel
Smooth skin without scales
Groove in tongue directs water
Corselet
Groove in body for fins

Adaptations for high-speed swimming in tunas.

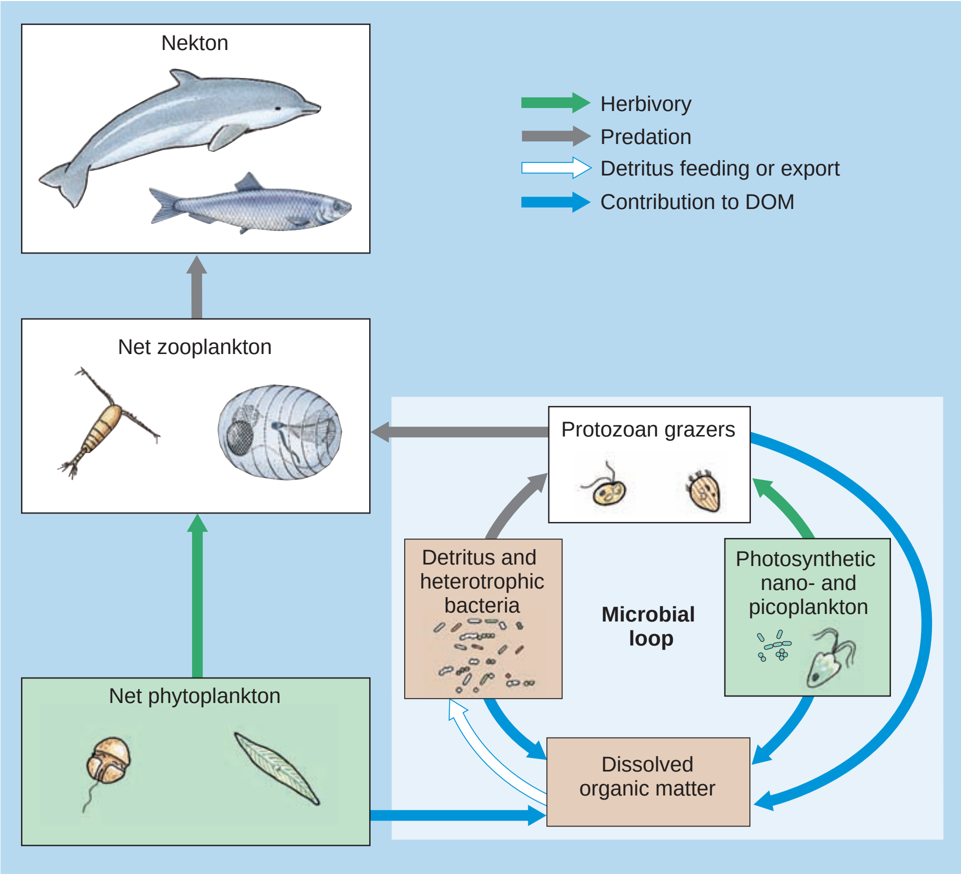


FIGURE 15.25 A modern view of epipelagic food webs. The left side of the diagram shows the flow of energy from the net phytoplankton to the nekton. This part of epipelagic food webs has been known for decades. The right side of the diagram shows the more recently discovered microbial loop. Much of the flow from organisms into dissolved organic matter (blue arrows) is caused by viruses.

mentioned: fecal pellets and abandoned larvacean houses. Larvacean houses and other accumulations of mucus can be very abundant and support rich populations of bacteria. They are often called **marine snow** because underwater they look like snowflakes.

Many zooplankton and small fishes eat marine snow. Much of the detritus, however, sinks out of the epipelagic zone to deeper zones before epipelagic organisms can use it. Furthermore, as previously noted, the epipelagic does not get much detritus from other systems.

Patterns of Production

Epipelagic food webs are complex, but they all share one simple feature: Primary production by phytoplankton, be they pico-, nano-, or net plankton, is the base. All other organisms, from the smallest zooplankton to the largest predators, depend on this primary production. Some parts of the epipelagic rank among the most productive ecosystems on earth (see Table 10.1, p. 225). There are also large areas that are among the least productive, the "deserts" of the ocean. The abundance of animals, from zooplankton to whales, generally follows the pattern of primary production (Fig. 15.26). It is therefore essential to understand the factors that control primary production by phytoplankton.

Phytoplankton need two main things to perform photosynthesis. First, they need sunlight, the ultimate source of energy for the ecosystem. Second, they need a supply of essential nutrients. Without sunlight and nutrients, phytoplankton cannot grow and produce the food that fuels the food web.

Light Limitation The epipelagic represents the sunlit layer of the ocean, but there is not always enough light for photosynthesis. In other words, primary production may be **light-limited.** There is no light at night, of course, so phytoplankton must get enough light during the day to allow them to grow. At high latitudes, phytoplankton may be light-limited during winter, when the days are short and the sunlight weak. In winter, phytoplankton at these latitudes store less energy in photosynthesis than they burn up in respiration. In tropical and subtropical waters, on the other hand, there is enough light to support photosynthesis throughout the year, at least at the surface.

The total primary production in the water column depends not only on the intensity of light at the surface, but also on how deep the light penetrates. If only a thin layer at the surface is sufficiently well lit for photosynthesis, there will not be as much production as if the photic zone were deep. The depth of the photic zone varies with the season, being deepest in summer. Photic zone depth also depends on the weather. On cloudy days, light does not penetrate as deeply as on bright, sunny days. Especially important is the amount of sediment and other material in the water. Light penetrates deeper in clear than in dirty water, so the photic zone is deeper. The phytoplankton themselves affect the depth of the photic zone. Because they absorb light to perform photosynthesis, the phytoplankton cut down the amount of light available to deeper-living phytoplankton. This phenomenon, known as **self-shading,** is especially important in highly productive waters, which are rather murky because they contain so much plankton. Conversely, the barren waters of the **central gyres,** in the middle of the ocean basins (see Fig. 3.20), are incredibly clear.

Nutrients Nutrients, especially nitrogen, iron, and phosphorus, play a major part in controlling primary production. Even with plenty of light, plants cannot perform photosynthesis if there are not enough nutrients, that is, if primary production becomes **nutrient-limited.** Over much of the ocean the nutrient in shortest supply, that is, the **limiting nutrient,** is nitrogen. **Nitrate (NO_3^{-1})** is the most important source of nitrogen. Oceanographers are increasingly concerned that human activities are adding huge amounts of nitrate and other forms of nitrogen to the ocean, with currently unknown but potentially devastating consequences. It is possible that the extra nitrogen will enhance fisheries or have other

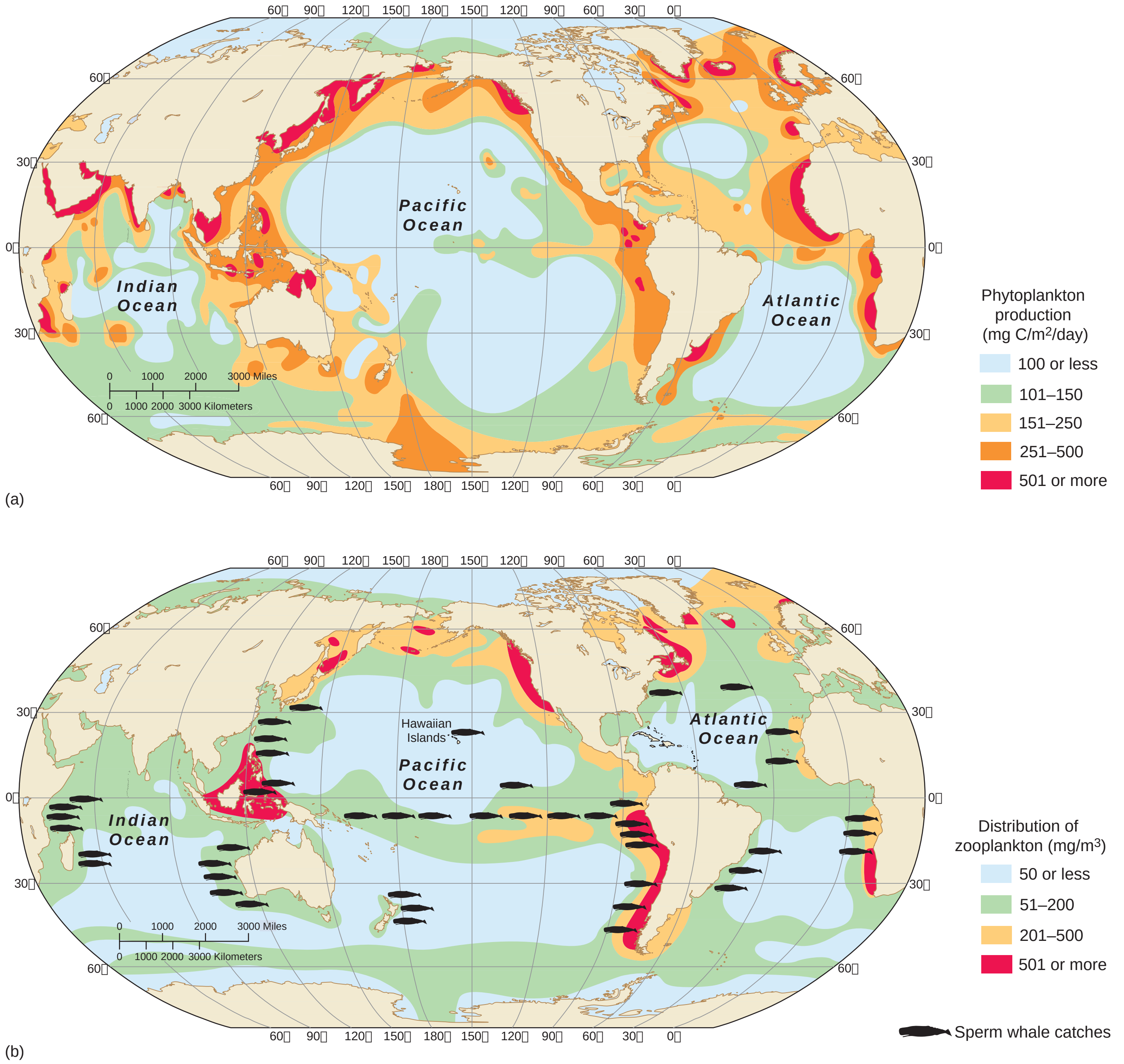

(a)
Pacific Ocean
Indian Ocean
Atlantic Ocean
60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60° 30° 0° 30° 60°
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
Phytoplankton production (mg C/m²/day)
100 or less
101–150
151–250
251–500
501 or more
(b)
Hawaiian Islands
Pacific Ocean
Indian Ocean
Atlantic Ocean
Distribution of zooplankton (mg/m³)
50 or less
51–200
201–500
501 or more
Sperm whale catches

FIGURE 15.26 (*a*) The distribution of average daily primary productivity in the oceans. Note the relationship of productivity to current and upwelling systems. Because primary production is the base of the food web, this pattern is reflected at higher levels, for example, in the average distribution of zooplankton (*b*) and of sperm whales, as indicated by whale catches from 1760 to 1926. Some areas with low primary production, such as the Hawaiian Islands, show high catches because of whale migration and the proximity to land bases.

beneficial impacts, but it could also lead to widespread increases in harmful algal blooms and hypoxic "dead zones" or disrupt food webs (see "Overwhelming the Nitrogen Cycle," p. 236).

Large areas of the open ocean, including the Southern Ocean (see Fig. 2.2) and the equatorial south Pacific are limited by iron instead of nitrogen. This has been demonstrated in dramatic experiments where phytoplankton grow explosively after iron is added, becoming so abundant they turn the water pea-soup green. There are highly controversial proposals to attempt to reduce global warming by fertilizing these parts of the ocean with iron, so that the resulting huge phytoplankton blooms would remove carbon dioxide (CO_2) from the atmosphere (see "So What Do We Do?" p. 239). Fertilizing the ocean with iron is more practical than using nitrate because much smaller amounts would be needed. Experiments to date, however, indicate that this "geoengineering" would not be very effective. The

EYE ON SCIENCE

International Studies of the Global Ocean

The vast Southern Ocean surrounding Antarctica supports a rich, unique ecosystem teeming with plankton and predators including seabirds, seals, and whales. The Southern Ocean also controls the nutrient supply to much of the rest of the oceans and influences global climate because of its sea ice and role in the flow of carbon dioxide and other gases between ocean and atmosphere. The pressing need to understand and predict global change, especially climate change (see "Special Report: Our Changing Planet," p. 231), makes it critical to understand the Southern Ocean ecosystem.

SO-GLOBEC is the Southern Ocean part of a major international research program, the Global Ocean Ecosystem Dynamics program. SO-GLOBEC has focused on Antarctic krill (*Euphausia superba*; see Fig. 17.12), the main food of many Antarctic predators (see Fig. 10.12), but instead of looking only at krill SO-GLOBEC has examined the entire ecosystem, including currents, weather and other physical features, and the krill's phytoplankton food, zooplankton competitors, and predators including penguins, seals, and whales. Studies of ocean circulation and chemistry, the abundance and growth of plankton, and the behavior, physiology, and reproduction of krill and their predators have begun to provide a picture of how variations in climate and ocean conditions flow through the food web from phytoplankton to whales. SO-GLOBEC researchers have discovered unexpected "hot spots" where krill, penguins, seals, sea birds, and whales are all abundant, have shown how the health and breeding success of predators like Adélie penguins (*Pygoscelis adeliae*) and crabeater seals (*Lobodon carcinophagus*) depends on the supply of krill, and have revealed that krill populations in some areas have declined over the last several decades, with a corresponding increase in a salp competitor (*Salpa thompsoni*). This could simply reflect a natural cycle or be a consequence of climate change.

Field work for SO-GLOBEC ended in 2007, but a successor is already underway. The Integrating Climate and Ecosystem Dynamics in the Southern Ocean (ICED) project will assist in planning upcoming surveys of krill populations and in analyzing SO-GLOBEC data, which will take until 2009, but ICED will also build upon SO-GLOBEC to broaden the range of studies. Krill research will continue, but other species will be studied in more detail not just as krill competitors but to learn their own role in the ecosystem—for example, their contributions to energy flow to higher predators. Another focus of ICED is the role of the Southern Ocean in global climate and nutrient cycles. Like SO-GLOBEC, ICED is an international effort of many countries, including Australia, Belgium, Britain, Canada, France, Germany, Japan, Korea, Russia, and the United States—an effort of this magnitude requires scientists and resources from around the world. ICED was launched in conjunction with the International Polar Year (March 2007–March 2008), but ICED studies of the great Southern Ocean that links all the other ocean basins will continue for at least a decade.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

ecological consequences can only be guessed at, and the risks to the planet are immense.

Phosphate (PO_4^{-3}) and various other nutrients also limit phytoplankton growth in some places or for some groups of organisms. The supply of silicon sometimes limits diatom growth, for example.

Some nutrients enter the ocean from rivers or the atmosphere (see Figs. 10.21 and 10.22). Some organisms supply nitrogen nutrients to the epipelagic by fixing free nitrogen (N_2). The colonial cyanobacterium *Trichodesmium* is the most important of these, especially in tropical waters where it accounts for more than half the total nitrogen fixation (Table 15.1). Some single-celled cyanobacteria have enyzmes needed to fix nitrogen, although it has not yet been demonstrated that they actually do so. Most of the nutrients that support the ocean's primary productivity, however, come not from new inputs but from nutrient recycling. The cycle begins when dissolved nutrients are incorporated into living organic matter by phytoplankton. Later, when the living material dies, the nutrients are **regenerated,** or released, as bacteria decompose the material.

The dependence on recycled nutrients profoundly affects production in the epipelagic. Much of the organic material produced by phytoplankton eventually ends up as detritus: fecal pellets, dead bodies, marine snow, and other organic particles. These organic particles tend to sink, and many sink out of the epipelagic into deeper waters before they decay. The nutrients they contain are released below the photic zone (Fig. 15.27). The net result of this process is that nutrients are removed from the surface and carried to the dark, cold waters below. Thus, surface waters are usually depleted in nutrients, and phytoplankton growth in the epipelagic is often nutrient-limited. Deep water, on the other hand, is usually nutrient-rich, but there is not enough light for photosynthesis and the nutrients cannot be used in primary production. The general nutrient profiles shown in Figure 15.28 are characteristic of most of the pelagic realm.

Because many organic particles sink out of the epipelagic before the nutrients they contain are regenerated, surface waters are poor in nutrients, and phytoplankton growth is often nutrient-limited. Deep waters are high in nutrients because of the rain of organic particles from the surface.

The phytoplankton that support epipelagic food webs, then, have a problem: At the surface there is sunlight but hardly any nutrients, whereas in deep water there are plenty of nutrients but not enough light. Neritic phytoplankton have it somewhat easier than oceanic forms. Neritic areas are relatively shallow, so the bottom traps sinking organic particles and some of the regenerated nutrients are returned to the water column. This is one reason the continental shelves are highly productive. Another reason is that rivers bring in fresh nutrients from land. Even so, neritic waters may have very low surface concentrations of nitrate, phosphate, and other nutrients.

Neritic waters are usually highly productive because the shallow bottom holds organic particles and the nutrients they contain near the photic zone and because rivers bring in additional nutrients.

For primary production to occur in oceanic areas, the nutrients contained in the deep water must somehow get to the surface. The only effective way for this to happen is for the water itself to move to the surface, carrying the nutrients along with it. This sounds simple enough, but it occurs only at certain times and places. The ocean is usually **stratified;** that is, warm surface layers float on the denser water below (see "The Three-Layered Ocean," p. 53). A **thermocline,** a zone of transition, lies between the warmer, less dense layer at the surface and the colder, denser layer below. Just as energy is needed to push a cork below the surface or lift a weight up from the bottom, it takes energy to push surface water down across the thermocline into the denser water below, mixing it with the deep water, or to bring dense, nutrient-rich deep water to the surface. Much of the time this simply doesn't happen, and surface production is often nutrient-limited.

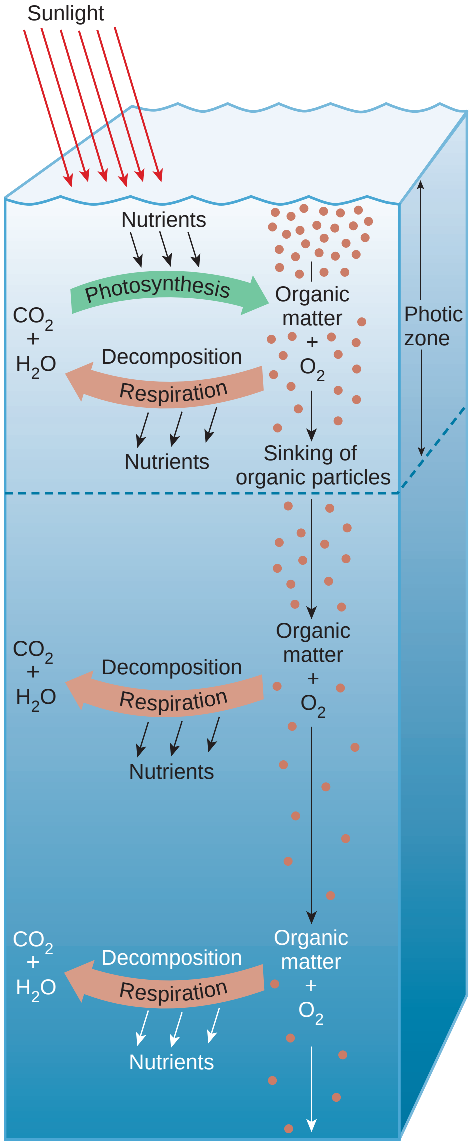


FIGURE 15.27 The amount of nutrients at different depths is controlled by photosynthesis, respiration, and the sinking of organic particles. In primary production, dissolved nutrients are removed from the water and incorporated into organic matter. Respiration, in this case mainly by bacterial decay, breaks down the organic matter and regenerates the nutrients. The uptake of nutrients can occur only at the surface, where there is light. Because organic particles sink, however, much of the regeneration occurs below the photic zone. This process strips nutrients from the surface layer and carries them into deeper water.

Seasonal Patterns One way that deep-water nutrients get to the surface is for the water column to mix. On the continental shelf, strong wind and waves may mix the water column all the way to the bottom. Often, however, wind and waves do not mix the water deeply enough to bring nutrients to the surface, especially in the open ocean.

If the surface water gets denser, however, it loses its tendency to float. In the ocean this happens at high latitudes when winter cold and winds cool the surface water. If the surface water gets denser than the water below, **overturn** occurs (see Fig. 3.23). The thermocline breaks down, the surface water sinks, and nutrient-rich deep water is mixed up to the surface. Overturn depends on very cold conditions and is not usually widespread except in polar waters. Even in the absence of overturn, however, surface cooling can promote mixing. Since the cooler surface water becomes more dense, less energy is needed to mix it with the deep water. The mixing of deep nutrients to the surface is assisted by winter storms, which bring strong winds and large waves. Because of

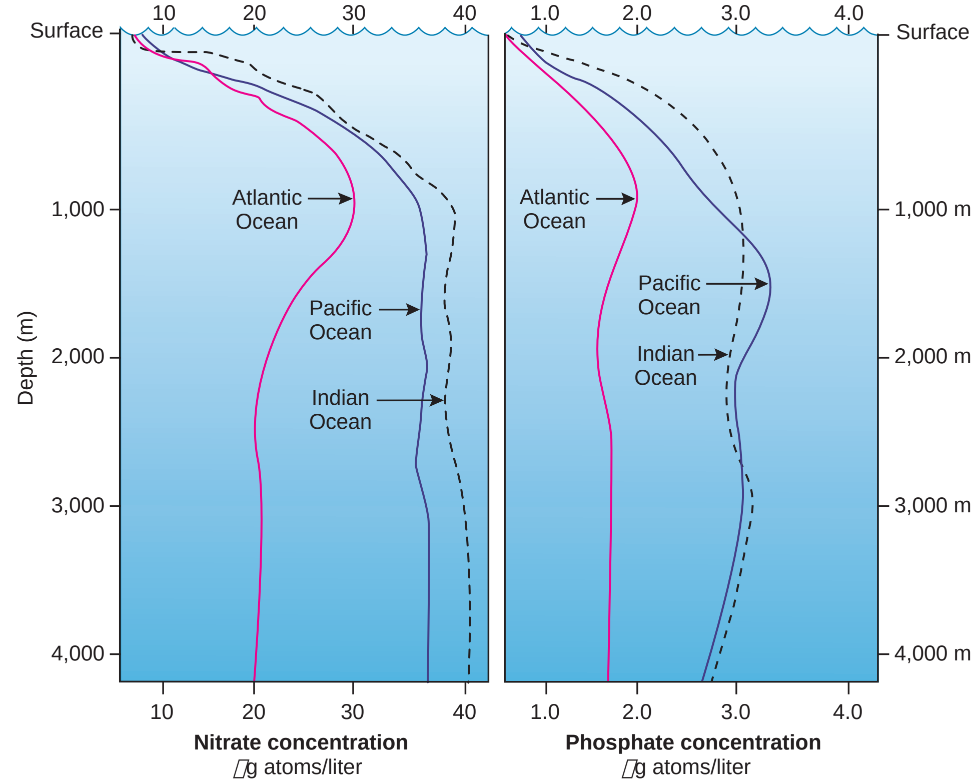


FIGURE 15.28 Typical profiles of nitrate and phosphate in the open ocean. Note that surface waters generally have very low levels of these nutrients.

overturn and mixing during the winter, polar and temperate waters are highly productive (Fig. 15.26).

> Oceanic waters at high latitudes are highly productive because winter overturn and mixing bring nutrient-rich deep water to the surface.

The productivity figures in Figure 15.26 and Table 10.1 (p. 225) refer to production over the entire year. This obscures the fact that primary production often varies during the year. In warm temperate and tropical waters such seasonal variation is relatively small. The water column remains stable throughout the year, restricting the transport of deep nutrients up into the photic zone. For this reason, most tropical waters have low but fairly constant levels of production throughout the year (Fig. 15.29*a*).

In temperate waters the effects of the seasons are profound. Overturn and mixing during the winter bring large amounts of nutrients to the surface. The phytoplankton are light-limited in winter, however, and unable to use the nutrients in photosynthesis. Primary production during winter months, therefore, is low at temperate latitudes (Fig. 15.29*b*).

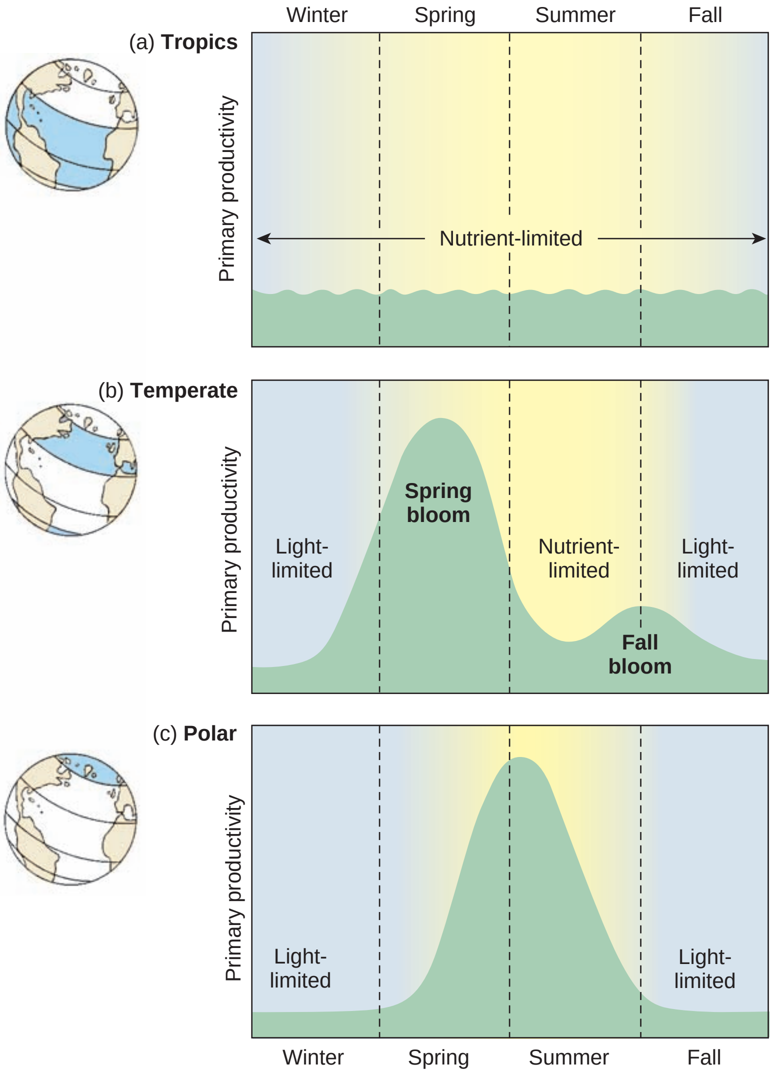


FIGURE 15.29 Generalized seasonal cycles of primary productivity (mg C/m^2/day) in (*a*) tropical, (*b*) temperate, and (*c*) polar waters.

When spring comes, the days get longer and the sunshine more intense. Light is no longer limiting, and the surface water contains plenty of nutrients because of overturn and mixing during the preceding winter. The availability of both light and nutrients provides ideal conditions for phytoplankton and produces a period of rapid growth called the **spring bloom** (Fig. 15.29*b*). In many temperate areas the spring bloom represents most of the primary production for the entire year.

As the spring bloom develops, two things occur, neither beneficial for phytoplankton growth. First, the increase in sunlight warms the surface water, making it less dense. This increases the stability of the water column, eliminating overturn and greatly reducing the mixing of nutrient-rich deep water to the surface. Second, the phytoplankton rapidly use up nutrients as they photosynthesize and grow. Thus, nutrients are removed from the water at the same time that the supply is blocked. The amount of available nutrients in the water falls, and the phytoplankton become nutrient-limited. Nitrate is usually the nutrient that runs out first.

During most of the summer, primary production is nutrient-limited. The level of production depends on nutrient recycling and the new input of nutrients. If the water column never becomes very stable, some mixing and therefore some production takes place. If the surface water warms considerably and the water column becomes stratified, nutrient input by mixing is low and primary production falls. Temperate waters generally have low productivity during the summer months because of stratification.

Production in autumn depends largely on which comes first: the short days and weak sunlight that bring light limitation, or surface cooling and storms, which increase mixing of nutrients. If the days are cool and sunny, for example, a strong wind can mix up nutrients while the phytoplankton still have enough light to grow. If so, there will be a burst of production known as the **fall bloom** (Fig. 15.29*b*). If warm, mild conditions persist late into the fall the phytoplankton become light-limited before overturn and mixing begin. Even though production at high latitudes is light-limited during the winter and nutrient-limited during the summer, enough production takes place during blooms to give these waters a high average over the year (Fig. 15.26).

> At high latitudes, primary production shows a seasonal cycle. During winter, production is light-limited but overturn and wind mixing bring nutrients to the surface. In spring, increased sunlight allows the phytoplankton to use the nutrients and a spring bloom occurs. During summer production is nutrient-limited because the phytoplankton use up the nutrients and stratification prevents mixing. A fall bloom occurs if stratification breaks down while there is enough light for photosynthesis.

Cold polar waters may not become stratified at all and may continue to produce at very high levels throughout the short summer when the sun shines most of the day (Fig. 15.29*c*). Primary production falls as the days shorten and is greatly reduced due to light limitation during the long winter months. Polar waters can be extremely productive, as is true in some parts of the Southern

Ocean. Production in much of the Southern Ocean, however, is limited by a shortage of iron. The Arctic Ocean lies at such a high latitude and is so extensively covered by ice that it is generally light-limited and unproductive in spite of overturn and mixing.

Upwelling and Productivity Overturn and mixing caused by the cooling of surface waters are not the only processes that transport nutrients up into the photic zone. At certain times and places large amounts of nutrient-rich water move up to the surface from below. This phenomenon, known as **upwelling,** is caused by **Ekman transport.**

Along some coasts, mainly on the eastern sides of the ocean basins, the prevailing winds blow parallel to the coast in a direction that causes Ekman transport to carry the surface layer offshore. At the edge of the continental shelf deeper water moves up to the surface to replace it (Fig. 15.30), typically from a depth of 50 to 300 m (165 to 1,000 ft). When this intense **coastal upwelling** comes from deep enough to tap into cold, nutrient-rich waters below the surface, it carries huge amounts of nutrients into the photic zone. Major coastal upwelling areas (Fig. 15.31) are among the most productive waters of the epipelagic (Fig. 15.26) and therefore are among the richest fishing grounds (see Fig. 17.4).

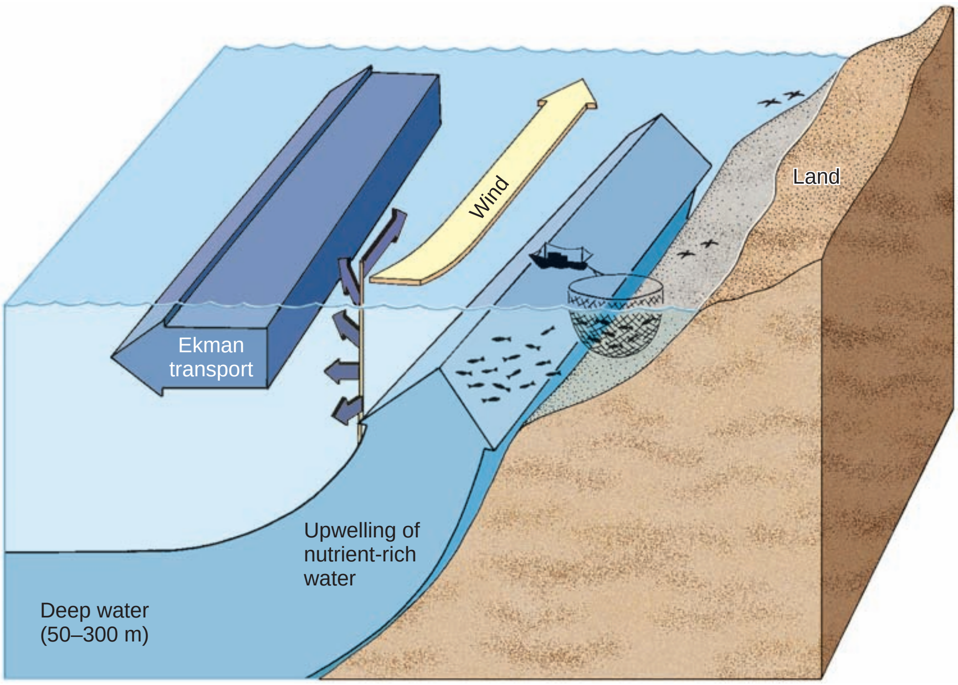
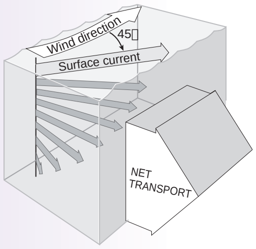

Wind
Land
Ekman transport
Upwelling of nutrient-rich water
Deep water (50–300 m)

FIGURE 15.30 When prevailing winds blow in the right direction along the coast, Ekman transport carries surface water offshore. Deeper water rises into the photic zone, carrying nutrients with it. This phenomenon is called coastal upwelling. Is the example in this figure from the Northern or Southern Hemisphere?

Ekman Transport The net movement of the upper layer of the water column, or *Ekman layer,* at 90° to the wind direction, to the right in the Northern Hemisphere and the left in the Southern Hemisphere. This occurs as a result of the *Coriolis effect.*

- Chapter 3, p. 50


Wind direction
45°
Surface current
NET TRANSPORT

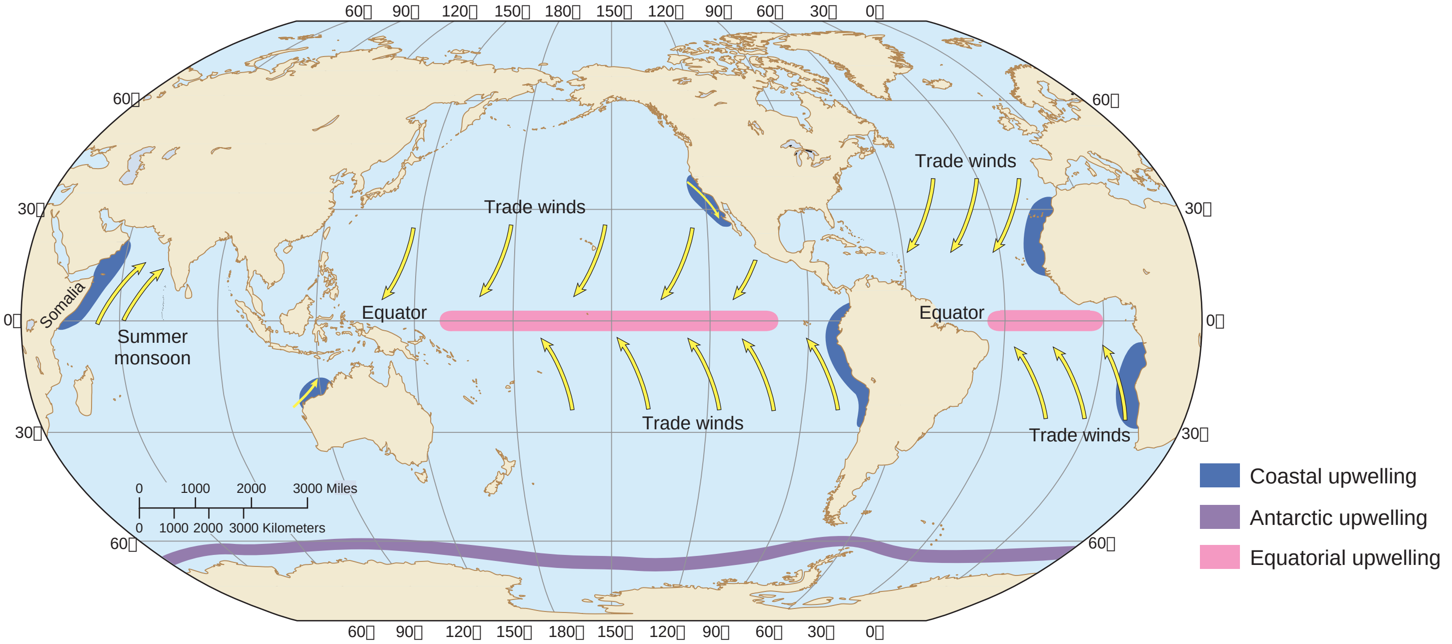

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
60°
30°
0°
30°
60°
Trade winds
Trade winds
Somalia
Summer monsoon
Equator
Equator
Trade winds
Trade winds
0 1000 2000 3000 Miles
0 1000 2000 3000 Kilometers
Coastal upwelling
Antarctic upwelling
Equatorial upwelling

FIGURE 15.31 The major upwelling areas of the world in relation to the prevailing winds. These areas are among the most productive parts of the ocean (see Fig. 15.26). Less intense or more sporadic upwelling occurs in many other areas.

On some coasts, like the Pacific coast of South America, upwelling is fairly steady and takes place over a large geographic area. On other coasts, like that of California, upwelling tends to occur as localized, short-lived events (Fig. 15.32). If the wind is strong for a few days, strong upwelling occurs, only to fade away when the wind dies and spring up somewhere else. Even on the Pacific coast of South America, upwelling is usually most intense in small, localized patches.

Upwelling also tends to be seasonal, occurring mainly during the time of year when winds are strong and blow in the right direction along the coast. Such seasonality is most pronounced on the coast of Somalia, in eastern Africa (Fig. 15.31). This area is dominated by **monsoons,** strong winds that blow northward in summer and southward in winter. The summer monsoon causes very intense coastal upwelling, which dies when the winds change to the winter monsoon. When the upwelling stops, production falls dramatically.

Coastal winds are not the only source of upwelling. The Coriolis effect also produces **equatorial upwelling,** especially in the Pacific. Note that the direction of the Coriolis effect changes from right to left at the Equator. Thus, the north equatorial currents transport surface water to the right (north), whereas the south equatorial currents transport water to the left (south; Fig. 15.33). In equatorial regions the sea surface is being pulled apart, or diverging, and deep water moves up to fill the void, typically from a depth of a few hundred meters. Equatorial upwelling is not as intense as coastal upwelling, but it still raises primary production significantly and occurs over much larger areas.

Upwelling also occurs in a ring around Antarctica as a result of complex wind and current patterns between the continent and the Antarctic Circumpolar Current (see Fig. 3.20). While coastal and equatorial upwelling typically come from depths of a few hundred meters at most, Antarctic upwelling brings water from as deep as 4,000 m (12,000 ft) to the surface. This upwelling, along with the relative lack of stratification (see "Seasonal Patterns," p. 349), contributes greatly to the high productivity of the Southern Ocean.

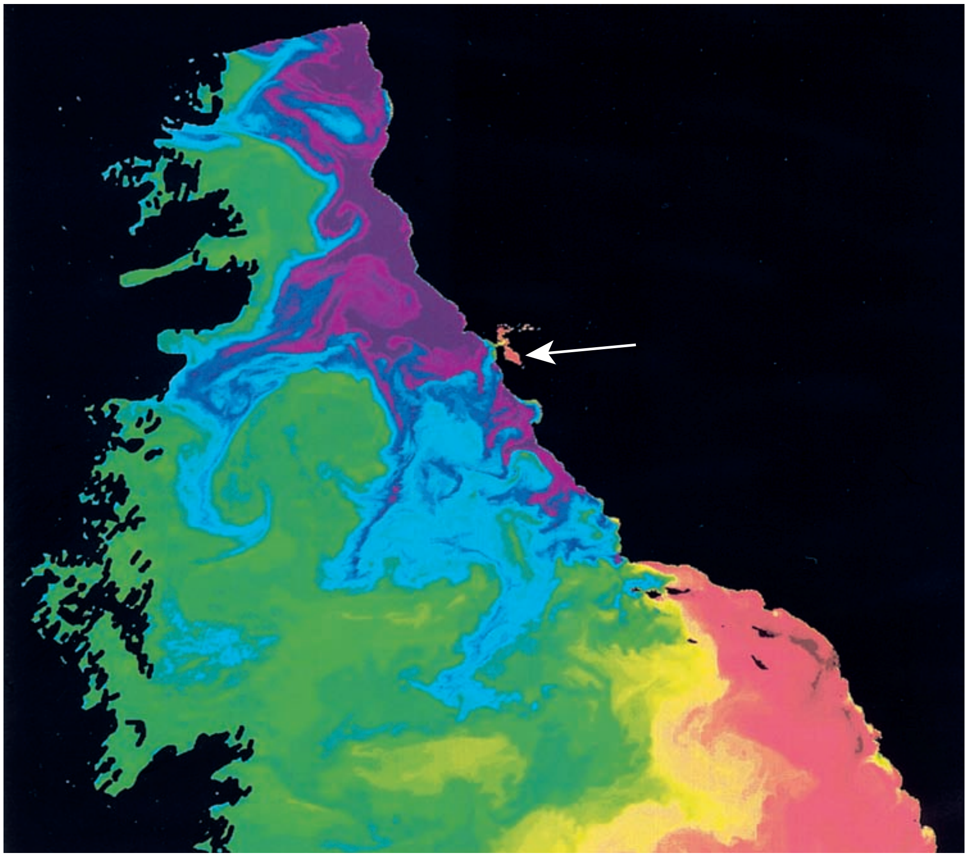


FIGURE 15.32 This satellite image shows summer upwelling along the California and southern Oregon coast. The red area in the lower right is warm surface water off Southern California. The purple water to the north is very cold deep water that has upwelled along the coast. Water farther offshore (green) is warmer. The small red patch near the center of the image (arrow) is San Francisco Bay. The black area to the left was obscured by clouds from the satellite's view and the black area on the right is land.

Upwelling brings nutrients to the surface and results in high primary production. Coastal upwelling is very intense. It occurs when winds cause the Ekman transport of surface water offshore. Equatorial upwelling is caused by the divergence of equatorial surface currents. Antarctic upwelling occurs in a ring around Antarctica and brings very deep water to the surface.

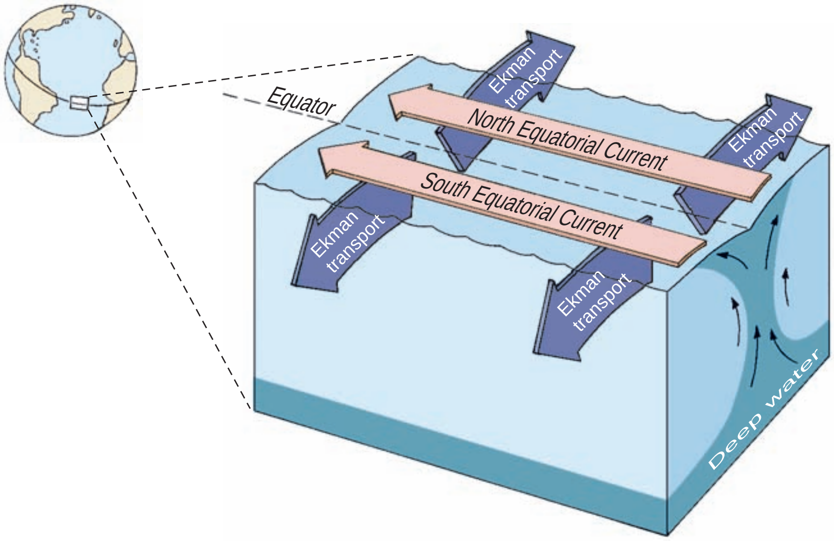


FIGURE 15.33 The Coriolis effect influences the equatorial currents differently on opposite sides of the equator. Surface water therefore moves away from the equator. To replace it, deep water moves up into the sunlit zone. This is called equatorial upwelling (see Fig. 15.26).

Geographic Patterns Water depth and temperature, prevailing winds, and surface currents all affect the ocean's productivity, as we have seen in the previous sections. The geographic distribution of productivity (Fig. 15.26) reflects these factors. Coastal waters are highly productive because the shallow bottom prevents nutrients from sinking out of the photic zone and because wind and waves mix the water column. Coastal areas that experience upwelling are especially productive. Equatorial waters, too, are productive because of upwelling, but not as productive as coastal upwelling zones. Polar and cold temperate regions have high productivity because overturn and upwelling bring nutrients up into the sunlit layer.

None of the processes that bring nutrients to the surface operate in the vast central gyres. These lie in relatively warm latitudes, so the surface waters never cool enough for overturn or mixing. Far from both the coast and the equatorial currents, the central gyres never experience upwelling, either. The gyre regions are permanently limited by nutrients; with the exception of the light-limited Arctic Ocean, they have the lowest productivity in the epipelagic. In fact, the central gyres are among the least productive ecosystems on earth (see Table 10.1, p. 225).

The El Niño–Southern Oscillation Phenomenon

The interplay of winds, currents, and upwelling affects not only the ocean's primary production, but also fisheries, climate, and ultimately human welfare. This is brought home most strongly when normal patterns suddenly change, as in the phenomenon known as the **El Niño–Southern Oscillation (ENSO).** In recent years ENSO, often simply called El Niño, has received widespread attention not only from marine scientists but also, because of its impact on humans, from economists, politicians, and the general public.

The term "El Niño" originally referred to a change in the surface currents along the coasts of Perú and Chile. For much of the year the winds along this coast blow from south to north, producing strong upwelling. The upwelling brings nutrients to the surface, making these waters one of the world's richest fishing grounds. Every year, usually in December, the trade winds slack off, upwelling decreases, and the water gets warmer. Locals have been familiar with this event for centuries because it signals the end of the peak fishing season. Because this change in currents comes around Christmas, they called it *El Niño,* or "The Child." Every few years, however, the change is much more pronounced than usual. The surface water gets much warmer, and upwelling ceases completely. Primary production drops to almost nothing, and the fishes that normally teem in these waters disappear. Fisheries along the Perú-Chile coast are devastated, and seabirds die in huge numbers (see "Of Fish and Seabirds, Fishers and Chickens," p. 389).

The "Southern Oscillation" part of ENSO has also been known for a long time. Like El Niño, the Southern Oscillation was first noted because of its impact on humans. People in India depend on the summer monsoon winds to bring rain for their crops. Sometimes the monsoons fail, producing famine and hardship. Beginning in 1904, a British administrator named Gilbert Walker set out to predict when the monsoons would fail by analyzing weather records from around the world. He never achieved his goal, but he did discover a major atmospheric phenomenon that he named the Southern Oscillation.

The Southern Oscillation refers to a long-distance linkage in atmospheric (or barometric) pressure. When the pressure is high over the Pacific Ocean, it tends to be low over the Indian Ocean, and vice versa (Fig. 15.34). Over a period of months or years, the

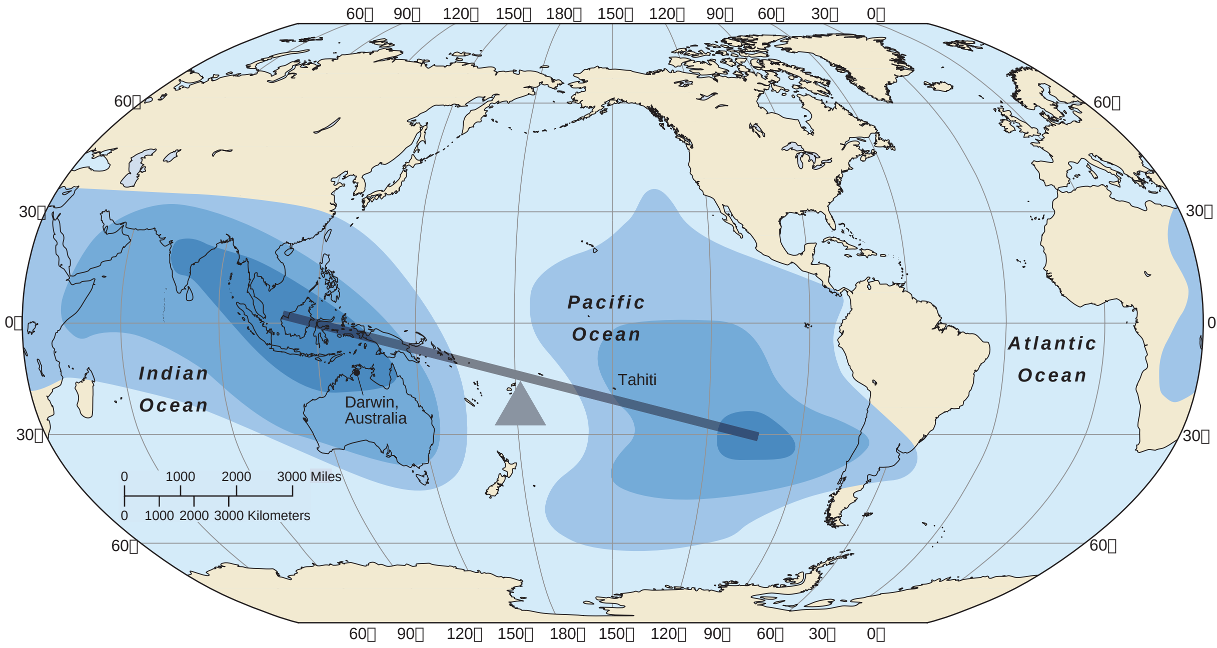


FIGURE 15.34 In the Southern Oscillation, atmospheric pressure "seesaws" between two gigantic systems half a world apart. When the pressure is unusually high in the western Pacific, it tends to be unusually low over the Indian Ocean, and vice versa. The shaded areas represent the linked zones of atmospheric pressure. The darker the blue, the more closely the atmospheric pressure is linked to pressure on the other side of the oscillation.

air pressure swings back and forth like a giant seesaw that extends halfway around the world. The changes in atmospheric pressure bring dramatic changes in wind and rainfall, including the failure of the summer monsoon.

In the late 1950s it became apparent that El Niño and the Southern Oscillation were two sides of the same coin: Instead of being isolated phenomena in a particular region, they are part of a complex interaction of ocean and atmosphere that links the entire planet. El Niño corresponds closely to dramatic changes in the Southern Oscillation. Scientists use the term "ENSO" to signify that El Niño and the Southern Oscillation are two aspects of the same global phenomenon.

When the strongest El Niño in at least a century occurred during 1982 and 1983, it became clear that El Niño has profound global effects on weather, wildlife, and society. The 1982–83 El Niño brought extreme weather to much of the planet—storms and floods in some places, in others drought, forest fires, and heat waves. These extreme conditions focused scientific and public attention on understanding and dealing with El Niño.

In the ensuing years scientists carefully analyzed information from the 1982–83 El Niño, as well as milder El Niño events in 1986–87 and 1991–95. Based on what they learned, they developed a Pacific-wide system of oceanographic and atmospheric monitoring equipment in the hope of getting early warning of new ENSO events. The system was soon put to the test. In late 1996 there were early signs, and by early 1997 the prediction was official: Another El Niño was on its way.

The prediction turned out to be accurate, with a vengeance. The 1997–98 El Niño was one of the strongest known El Niños of all time, even stronger than the 1982–83 El Niño. Its severity caught even the scientists who predicted it by surprise, and the devastating effects were felt over much of the globe (Fig. 15.35). In Perú, Chile, and Ecuador the 1997–98 El Niño brought not only a failure to fisheries but also torrential rain and flooding. Southern California, parts of East Africa, and southern China also suffered severe floods. At the other extreme, Indonesia, New Guinea, Australia, southern Africa, Central America, and the Amazon basin suffered droughts. In some places the opposing effects of flooding and drought occurred over very short distances. Bolivia, for example, had drought in highland areas, but floods in the lowlands. The inland areas of southern and central Mexico were also afflicted by drought, but the Pacific coast was lashed by hurricanes. The Caribbean and southeastern United States enjoyed a mild hurricane season because El Niño causes changes in jet stream winds. The 1997–98 El Niño, however, brought such drastic weather changes that swarms of killer tornados struck central Florida, where they are usually uncommon. Worldwide, several thousand people at least were killed in floods and storms.

The El Niño also had many secondary effects. Crop and livestock losses were enormous, bringing hardship to farmers, especially in poorer countries, and in some places famine. The financial losses from agricultural failure amounted to hundreds of millions of dollars, and markets were affected widely as prices rose because of reduced supply. The fisheries crash in Perú and Chile had

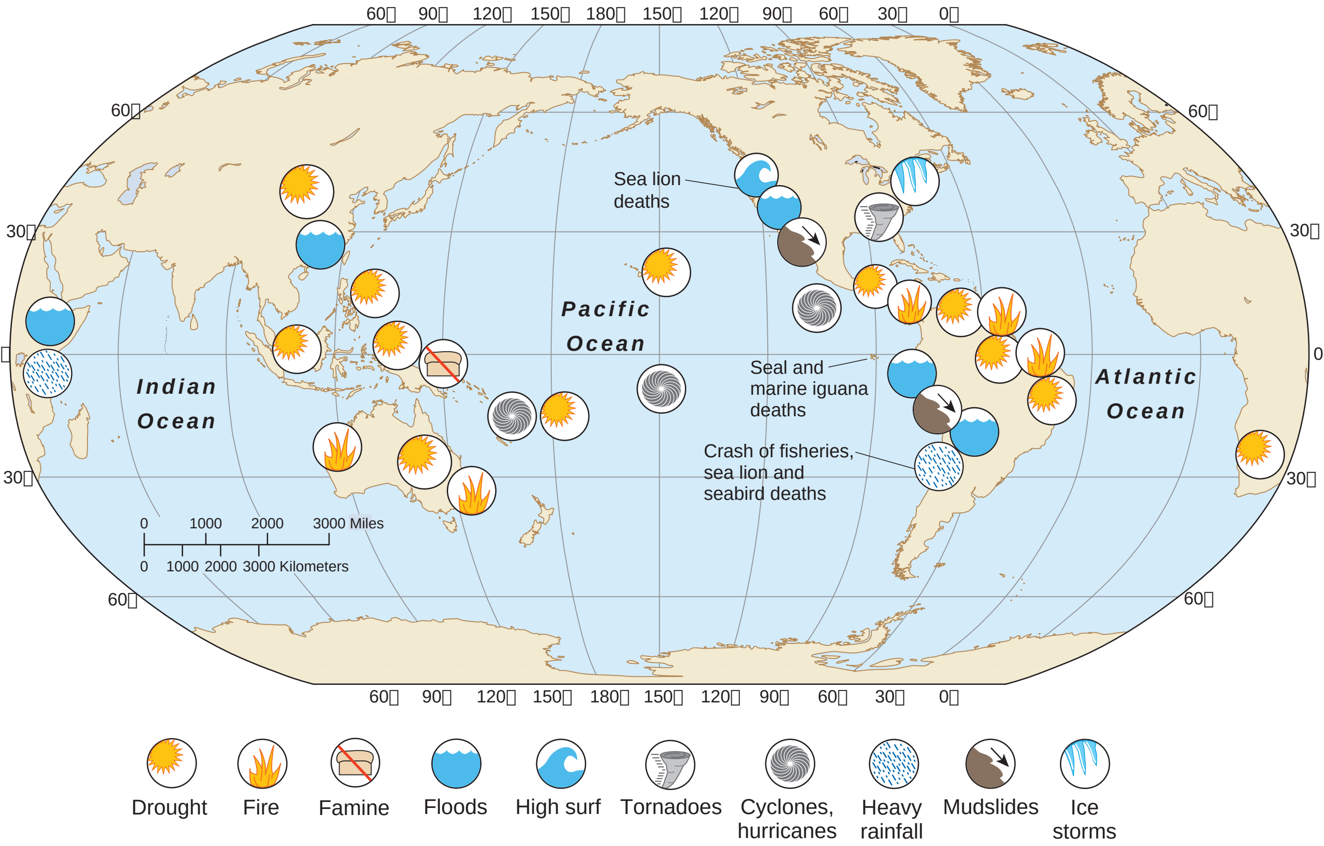


FIGURE 15.35 Some of the worldwide events linked to the 1997–98 El Niño event. This is just a sampling; many other places were affected.

similar effects: Much of the catch is processed into animal feed and farmers as far away as Ireland faced higher feed prices. Fires, often lit by farmers using the opportunity to clear land, raged out of control in drought-stricken Indonesia and the Amazon basin. Thousands of square miles of rain forest were destroyed. The fires in Indonesia were so bad that much of Southeast Asia endured months of haze and air pollution, and an accompanying increase in respiratory ailments. The thick smoke even caused several plane crashes. Mass coral bleaching occurred on many reefs around the world (see "Light and Temperature," p. 308).

Disease outbreaks from water contamination sometimes followed storms and floods. Warmer temperatures led to increases in mosquito-borne diseases like malaria, encephalitis, and dengue fever. In North America, outbreaks of bubonic plague and an often fatal respiratory disease known as hantavirus are associated with severe El Niños. This is because the growth in vegetation after the high rainfall provides more food for rats and mice, which spread the diseases. There were even more unusual problems. After its floods were over, for example, Kenya suffered a plague of a kind of beetle that, when crushed, releases a poison that causes burning, itching, and blindness.

The effects of El Niño are not necessarily all bad, or at least not bad for everyone. Cyclone activity was down in Hong Kong and the Philippines, as were hurricanes in the Caribbean. Farmers lucky enough to escape El Niño's wrath enjoyed higher prices for their crops. In Chile and the southwestern United States, heavy rains filled dams and replenished water supplies. Heavy snowfall delighted skiers and resort owners. Deserts bloomed when the rains brought spectacular displays of wildflowers. Indeed, El Niño's periodic soakings may be a vital part of desert ecology. El Niño brought a relatively mild winter to much of the northern United States and Europe, saving millions of dollars on heating bills. While the normal fisheries in Perú and Chile crashed, warm-water fishes like dolphin and tunas appeared in record numbers. Salmon fishers in Oregon even caught striped marlin, normally confined to the subtropics.

The effects of ENSO are harmful not so much in and of themselves as because they are extreme changes in the normal pattern. Heavy rain where it is rare may cause floods, while the lack of heavy rain in places that depend on it causes drought and famine. Indeed, scientists now realize that El Niño is not really an abnormal occurrence, but simply one extreme of a regular weather cycle. **La Niña,** the other extreme, brings weather conditions that are roughly the opposite of El Niño's. Places that experience drought during El Niño, for example, can expect wet weather during La Niña years. After a mild hurricane season during the 1997–98 El Niño, Central America and the Caribbean suffered devastating hurricanes in the La Niña that followed. Another major cycle, the North Atlantic Oscillation, has been found to profoundly influence Europe's weather.

Damage estimates from the record-breaking El Niño of 1997–98 range upward of $20 billion, but it could have been much worse. Because scientists could predict El Niño the world had advance warning and time to prepare. Authorities in many countries intensified their disaster preparedness efforts and built up food reserves. Industry and especially agriculture adjusted their planning. Cattle ranchers in Australia, for example, reduced their herds, cutting the losses from the subsequent drought. In southern Africa farmers cut back their normal crop of corn and planted more drought-resistant plants. Every El Niño is different, however, and in a given place the exact effects are hard to predict. In 1997–98, for example, authorities in parts of East Africa expected drought based on past El Niños. Instead, they had terrible floods. Nonetheless, the ability to predict when El Niño is on the way has huge benefits for society.

As profound as the effects of El Niño are, it is important to recognize that not every unusual occurrence or spell of bad weather is caused by El Niño. During the 1997–98 event, some reports blamed El Niño for everything from political scandal to the Super Bowl winner! Weather patterns are naturally variable, and unusual weather sometimes happens whether there is an El Niño around or not.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Plankton are unable to swim effectively and drift about at the mercy of the currents. You might think that the currents would scatter planktonic organisms throughout the oceans, but many species are restricted to particular regions. What mechanisms might allow a species to maintain its characteristic distribution?
2. Spiny species of diatoms are found in both warm subtropical waters and colder areas. Because warm water is less dense than cold water, would you predict any differences between the spines of warm-water and cold-water individuals? Why?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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Wray, G. A., 2001. A world apart. *Natural History,* vol. 110, no. 2, March, pp. 52–63. The larvae of marine invertebrates have many adaptations for life in the plankton.

In Depth

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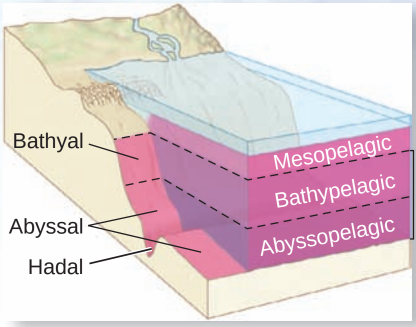
This deep-sea sea cucumber (*Scotoplanes*), common on many parts of the continental slope, "walks" along the bottom with its leg-like appendages.

16
CHAPTER

The Ocean Depths



"Inner space" it has been called. Dark and cold, inhabited by bizarre, fearsome-looking creatures, it *is* a little reminiscent of the outer space of science fiction movies. As in outer space, humans can venture into this mysterious realm only with the aid of elaborate, specially designed craft. Even then there is an element of risk. But "inner space" is here on Earth: It consists of ocean waters below the sunlit surface layer.

The ocean depths include a number of distinct habitats. Immediately below the epipelagic lies the **mesopelagic,** or "middle pelagic," **zone** (Fig. 16.1). The epipelagic is roughly equivalent to the **photic zone,** the surface layer down to 150 to 200 m (500 to 650 ft) where there is enough light to support primary production by photosynthesis. In the mesopelagic there is still some dim light, but not enough for photosynthesis. Below the mesopelagic there is no sunlight at all. This inky darkness is the world of the **deep sea.** The term "deep sea" is sometimes used to include the mesopelagic zone, but in this text we use it only for the perpetually dark waters below the mesopelagic.

The waters below the epipelagic can be divided into the mesopelagic zone, where there is some light but not enough for primary production, and the deep sea, where there is no sunlight at all.

Several different habitats are discussed in this chapter; each supports a distinct community of organisms. These communities

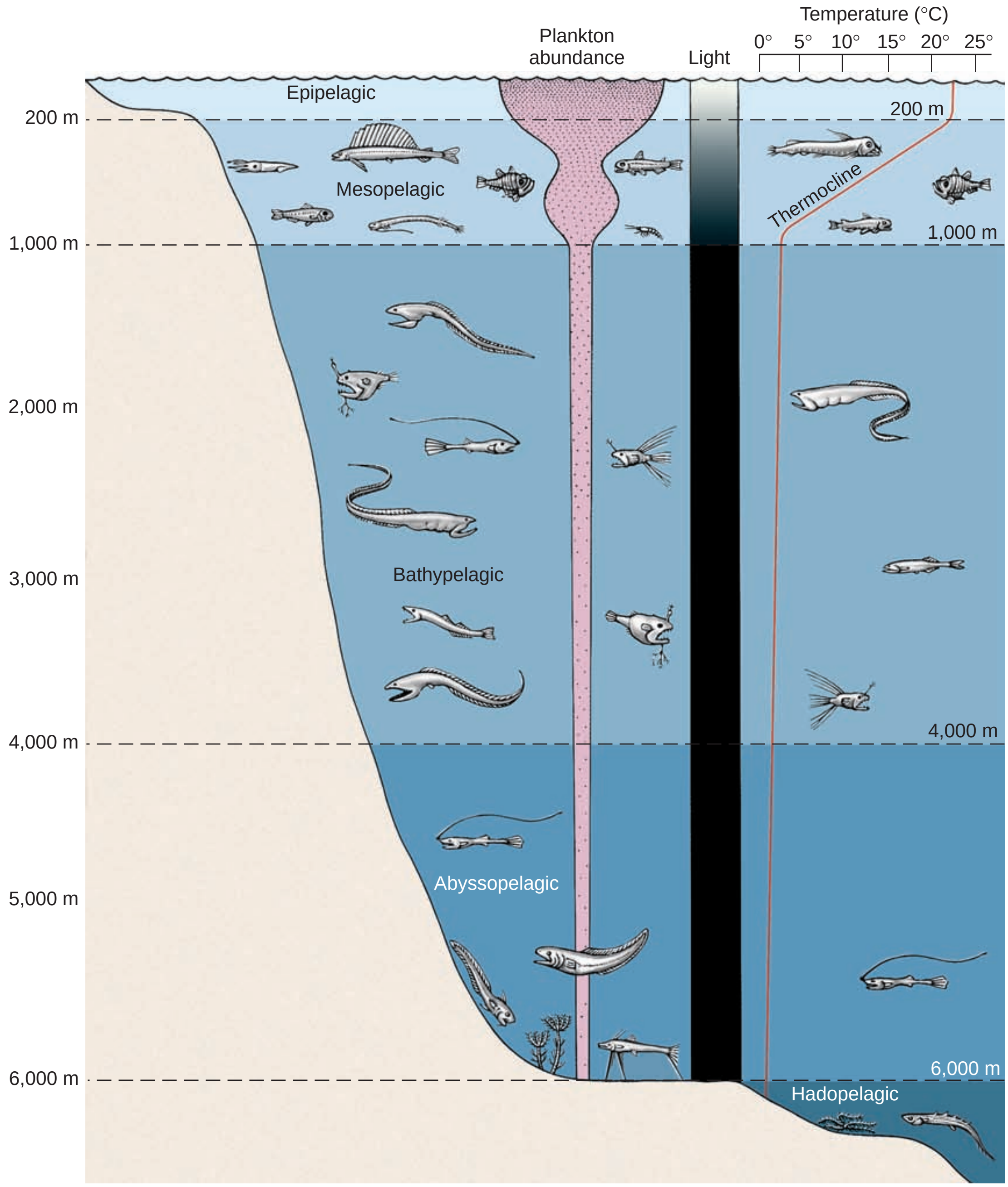

Plankton abundance
Light
Temperature (°C)
0° 5° 10° 15° 20° 25°
Epipelagic
200 m
200 m
Mesopelagic
Thermocline
1,000 m
1,000 m
2,000 m
3,000 m
Bathypelagic
4,000 m
4,000 m
5,000 m
Abyssopelagic
6,000 m
6,000 m
Hadopelagic

FIGURE 16.1 Life in the mesopelagic and deep sea is closely linked to the abundance of plankton and light intensity in the water column.

share one important feature: the lack of **primary production** of food by **photosynthesis.** Without primary production to support the rest of the food web, most of the communities beneath the photic zone depend for food on organic material produced in the surface layers of the ocean. Some of this surface production sinks into the dark waters below. Without a steady supply of food from above, there could be little life below the sunlit layer of the sea. Exceptions to this principle are discussed in the section "Hot Springs, Cold Seeps, and Dead Bodies" (p. 374).

Because of the dependence on surface production for food, life is much less abundant below the photic zone than in the sunlit surface layer. Most food particles get eaten before they sink into deeper water. With food in short supply, pelagic organisms become more and more scarce at greater depths. There are typically 5 or 10 times fewer organisms at 500 m (1,600 ft), for example, than there are at the surface, and perhaps 10 times fewer again at 4,000 m (13,000 ft).

Deep-water organisms depend on the surface not only for food, but also for oxygen (O_2). If the ocean were stagnant, the oxygen below the surface would be quickly used up by **respiration** and animal life would be impossible. Fortunately, however, **thermohaline circulation** and the **great ocean conveyor** constantly replenish the supply of oxygen to the deep sea. Oxygen still becomes depleted in some places, but by and large the ocean depths have enough oxygen to support respiration.

THE TWILIGHT WORLD

The mesopelagic is a world of twilight. In the upper part of the mesopelagic the dim light during the day is enough to see by, but there is not enough light to support phytoplankton growth. As depth increases, of course, the sea gets darker. Eventually, typically at a depth of about 1,000 m (3,300 ft), there is no light at all. The absence of light marks the bottom of the mesopelagic zone, which thus stretches from the bottom of the epipelagic, around 200 m (660 ft) deep, to about 1,000 m deep.

The mesopelagic zone extends from about 200 m to about 1,000 m deep.

The temperature at a given depth in the mesopelagic generally varies much less than in the epipelagic. The mesopelagic, however, is the zone where the **main thermocline** occurs (see Fig. 16.1), so organisms that move up and down in the water column encounter large changes in temperature. Mesopelagic organisms that stay at about the same depth experience more constant temperatures.

The Animals of the Mesopelagic

Though phytoplankton and other photosynthetic organisms cannot grow in the dim light, the mesopelagic supports a rich and varied community of animals, which are often called **midwater** animals.

Zooplankton The major groups of animals in the mesopelagic zooplankton are much the same as those in the epipelagic (see "The Zooplankton," p. 331). **Krill** and **copepods** are generally dominant, as they are in surface waters. Several different kinds of shrimps (Fig. 16.2) are relatively more common in the mesopelagic than in the epipelagic. Krill and most mesopelagic shrimps have a common adaptation of midwater animals: **photophores,** or **light organs,** which are specialized structures that produce light. The function of this "living light," called **bioluminescence,** is discussed later (see "Bioluminescence," p. 365).

Primary Production The conversion of carbon dioxide into organic matter by *autotrophs,* that is, the production of food.
- Chapter 4, p. 68

Photosynthesis
$CO_2 + H_2O + \text{sun energy} \rightarrow \underset{\text{(glucose)}}{\text{organic matter}} + O_2$
- Chapter 4, p. 66

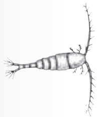
Respiration
$\underset{\text{(glucose)}}{\text{Organic matter}}\ O_2 \rightarrow CO_2 + H_2O + \text{energy}$
- Chapter 4, p. 67

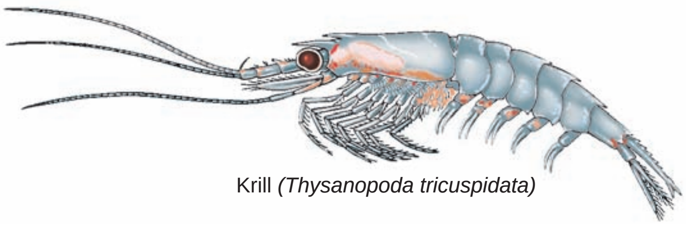
Thermohaline Circulation Ocean circulation that is driven by differences in water density, due to variations in water temperature and salinity, rather than by the wind or tides.
Great Ocean Conveyor A global circulation pattern in which water cycles throughout the ocean basins.
- Chapter 3, p. 53; Fig. 3.25

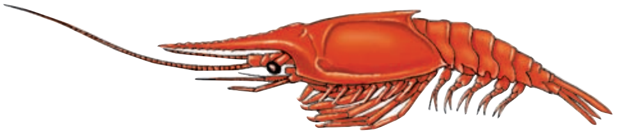
Main Thermocline The layer between about 200 and 1,000 m (650 and 3,300 ft) where the temperature drops rapidly as depth increases. This is a transition zone between the warm surface layers and the cold deep water.
- Chapter 3, p. 53; Figure 3.22

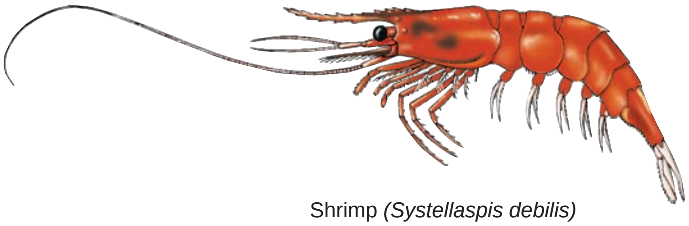
Krill Planktonic, shrimp-like crustaceans.
- Chapter 7, p. 136; Figure 17.2

Copepods Tiny crustaceans that are often planktonic.
- Chapter 7, p. 135




Krill *(Thysanopoda tricuspidata)*


Mysid shrimp *(Gnathophausia ingens)*


Shrimp *(Systellaspis debilis)*

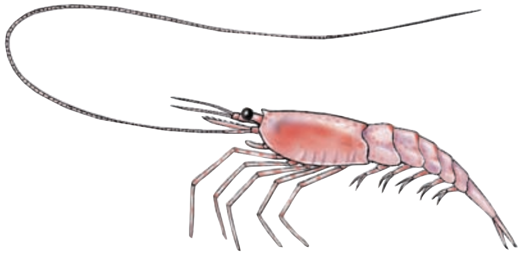

Shrimp *(Sergestes similis)*

FIGURE 16.2 Some crustaceans that inhabit the mesopelagic zone include krill; mysid, or opossum, shrimps; and true (decapod) shrimps like *Systellaspis debilis* and *Sergestes similis.*

The Chambered Nautilus

Nearly all cephalopods—the squids, octopuses, and cuttlefishes—have at most only vestiges of the hard shell that characterizes most other molluscs. Only a few species of chambered nautilus (*Nautilus*), the last living relatives of a group of animals that once ruled the seas, retain the large, heavy shell of their ancestors.

Most early animals in the sea lived on the bottom, crawling and scratching for survival. Around 500 million years ago a group of molluscs that looked something like today's limpets evolved a new trick: the ability to partially fill their shells with gas. Buoyed by the gas, these ancient ancestors of modern cephalopods, called nautiloids, were able to float up off the bottom away from predators. Before long they also developed the ability to move by squirting out water—probably the first form of jet propulsion.

These innovations were immensely successful. For 200 million years nautiloids and their descendants, especially a group with coiled shells called the ammonites, dominated the ocean. They had the water column more or less to themselves and could drop onto prey from above.

Then fishes, which had been around for some time, evolved a swim bladder. This allowed them to maintain neutral buoyancy and compete with the nautiloids. Fishes also could swim faster and more efficiently than the nautiloids, with their cumbersome shells. Outcompeted by fishes, most nautiloids went extinct. One group of cephalopods, the squids, became more fish-like. They abandoned the shell and became streamlined, active swimmers. Of all the heavy-shelled cephalopods, only *Nautilus* remains.

Nautilus lives in a coiled shell that is partitioned into a series of chambers. The chambers are walled off one by one as the animal grows. The animal lives only in the last chamber. The others are filled with gas and provide buoyancy, without which the heavy shell would drag the animal to the bottom. When the chamber is first partitioned it is filled with seawater. Rather than pumping gas in, *Nautilus* removes all the ions from the water in the chamber. This makes the water more dilute than the animal's blood, so the water flows into the blood by osmosis and gas diffuses into the chamber to replace it. After that the chamber is more or less sealed and doesn't need repeated filling and emptying like a fish's swim bladder. This allows *Nautilus* to move rapidly up and down in the water column.

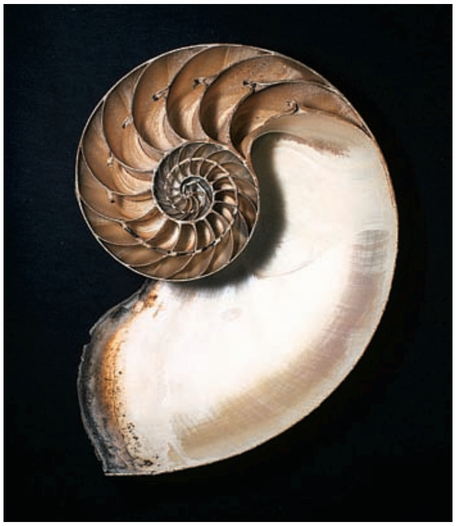
Nautilus is found near coral reefs but is not really a coral reef animal because it generally lives much deeper than corals, typically between 100 to 500 m (330 to 1,650 ft). It occasionally ventures into shallow water for short periods. The upper limit of its normal depth range is set by temperature; water temperatures above 25°C (77°F) are lethal, and those below 20°C (68°F) are preferred. If the water is cool enough *Nautilus* can live at the surface, and specimens can be maintained in aquaria. The lower depth limit is set by pressure. The shell chambers are sealed, so gas cannot be pumped in to counteract the pressure at great depth. Instead, the animal relies on the strength of its shell, like a submarine relies on the strength of its hull. When the pressure gets too great, at about 800 m (2,600 ft), the shell is crushed. Actually, water begins to leak into the chambers at shallower depths, and the animal probably doesn't spend much time at depths of even 500 m (1,650 ft).

Not much is known about *Nautilus.* It appears to be primarily a scavenger, locating animal remains and molted lobster shells by smell. Its neutral buoyancy reduces its energy expenditure as it moves up and down the water column looking for scent trails. When food is sensed, the animal swims to it by jet propulsion, squirting water out of a muscular funnel. It may also prey on live hermit crabs and other crustaceans. When not feeding it spends most of its time "asleep" in the cool, deep water, conserving energy. A single meal can last a *Nautilus* at least two months!

Interestingly, *Nautilus* can tolerate conditions of almost zero oxygen. It can use oxygen stored in the chambers of its shell, a trick evolved long before humans invented the scuba tank. The benefits of this ability are not known, since the waters where *Nautilus* lives normally have plenty of oxygen.

Another puzzle is that the vast majority of *Nautilus* caught in traps are males. Maybe females are hard to catch or in short supply. This remnant of an ancient group still holds plenty of secrets.

A chambered nautilus (*Nautilus belauensis*).



Longitudinal section of a shell of *Nautilus pompilius* showing the gas chambers.

A group of crustaceans known as **ostracods** can be very abundant in the mesopelagic. Ostracods have a characteristic shell, or **carapace,** that makes them look like tiny clams with legs (Fig. 16.3). They are crustaceans, however, and unrelated to clams. Like copepods, most ostracods are small, usually only a few millimeters (1/8 in) long. One group (*Gigantocypris*), however, can reach 1 cm (1/2 in). Amphipods and other crustaceans are also part of the midwater plankton.

Arrow worms, or **chaetognaths,** are important midwater predators. At times they are among the most abundant components of the midwater zooplankton, especially in the upper parts of the mesopelagic. Jellyfishes, siphonophores, comb jellies, larvaceans, and pteropods are also common. Most of the other major groups that are part of the epipelagic zooplankton are also represented in the mesopelagic, though the particular species are usually different.

Squids (Fig. 16.4) are also prominent members of the midwater community. Some swim only weakly and are planktonic, while strong-swimming squids are part of the nekton. Mesopelagic squids usually have photophores, typically arranged in a different pattern in each species. The vampire squid (*Vampyroteuthis;* Fig. 16.5) looks something like an octopus but is neither a squid nor an octopus and is in its own separate group. Like true squids, the vampire squid has photophores. There are also a few species of octopuses in the mesopelagic zone. Bioluminescence is not as common in mesopelagic octopuses as in squids, but some species do have photophores. One has light-emitting suckers.

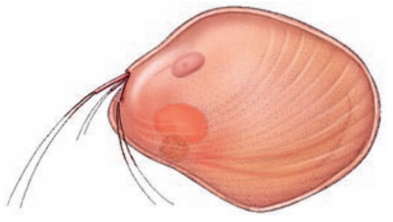


FIGURE 16.3 A mesopelagic ostracod (*Gigantocypris*). This one is about 1 cm (0.5 in) long. Most ostracods are much smaller.

Midwater Fishes Nearly all mesopelagic fishes are quite small, about 2 to 10 cm (1 to 4 in) long, although a very few species get considerably larger. Bristlemouths and lanternfishes (Fig. 16.6) are by far the most abundant fishes in the mesopelagic. These two groups may account for 90% or more of the fishes collected by midwater trawls (Fig. 16.7). Bristlemouths are the most common of all. One species (*Cyclothone signata*) is the most abundant fish on earth, which is both surprising and impressive when you consider the huge schools of fishes like sardines and herrings in the epipelagic. Bristlemouths are named for their many sharp teeth. They have rows of photophores on their underside, or ventral surface.

Lanternfishes get their name from the rows of photophores that adorn their heads and bodies. Like squids, each species typically has a distinctive photophore pattern. Lanternfishes have blunt heads, relatively large mouths, and large eyes, probably an adaptation to help them see in the dim light. They are very general in their food habits, eating just about anything they can get down.

The most common mesopelagic, or midwater, organisms are krill, copepods, shrimps, and small fishes like bristlemouths and lanternfishes.

Bristlemouths and lanternfishes are the most numerous, but many other fishes live in the mesopelagic. Marine hatchetfishes look somewhat like the unrelated freshwater hatchetfishes sold in pet shops, except for their large eyes and mouths and ventral photophores. Viperfishes, dragonfishes, barracudinas, sabertooth fishes, lancetfishes, snake mackerels, and cutlassfishes are all long, eel-like fishes with large mouths and eyes. Many have photophores, usually in rows on the ventral surface. Most are less than 30 cm (1 ft) long, but there are exceptions. One of the lancetfishes (*Alepisaurus ferox;* Fig. 16.6) grows to about 2 m (6.5 ft). The black scabbard fish (*Aphanopus carbo;* Fig. 16.8), a kind of cutlassfish, can get well over 1 m (3.3 ft) long.

Adaptations of Midwater Animals

By the standards of the surface world, many of the animals that live below the photic zone seem bizarre, indeed. Though they look strange to us, they are well adapted to their unique environment. Species from the same depth often have very similar characteristics even though they are unrelated. On the other hand, closely related species from different depths can differ markedly in appearance and other characteristics.

Feeding and Food Webs Most of the food produced in the epipelagic is used there; only about 20% of surface primary production sinks to the mesopelagic. This means that the mesopelagic is chronically short of food, which is why there are fewer

Arrow Worms or **Chaetognaths** Small, worm-like predators with fins along the body and spines on the head.

- Chapter 7, p. 140

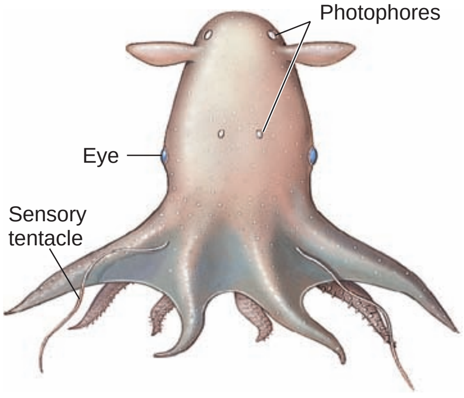


FIGURE 16.5 The vampire squid (*Vampyroteuthis infernalis*) differs from the closely related true squids in that two of its ten tentacles are modified into long, retractable "feelers," or sensory tentacles, instead of being used to capture prey. The vampire squid only grows to about 30 cm (12 in).

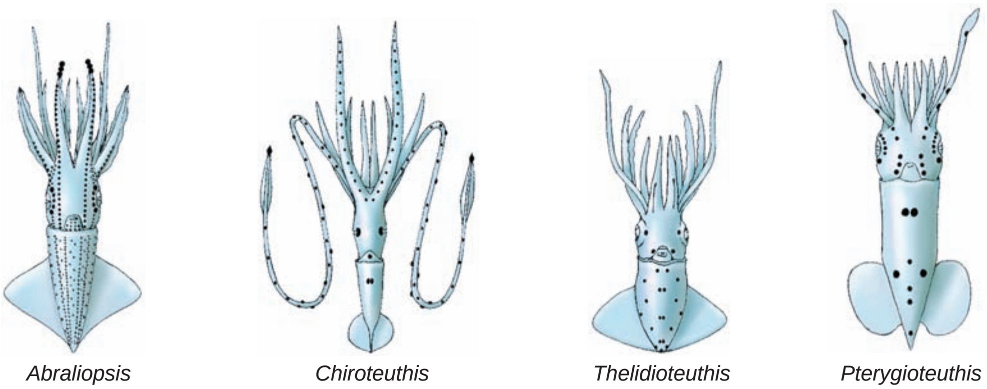


FIGURE 16.4 Most mesopelagic squids have photophores (shown in black), usually arranged in a different pattern in each species.

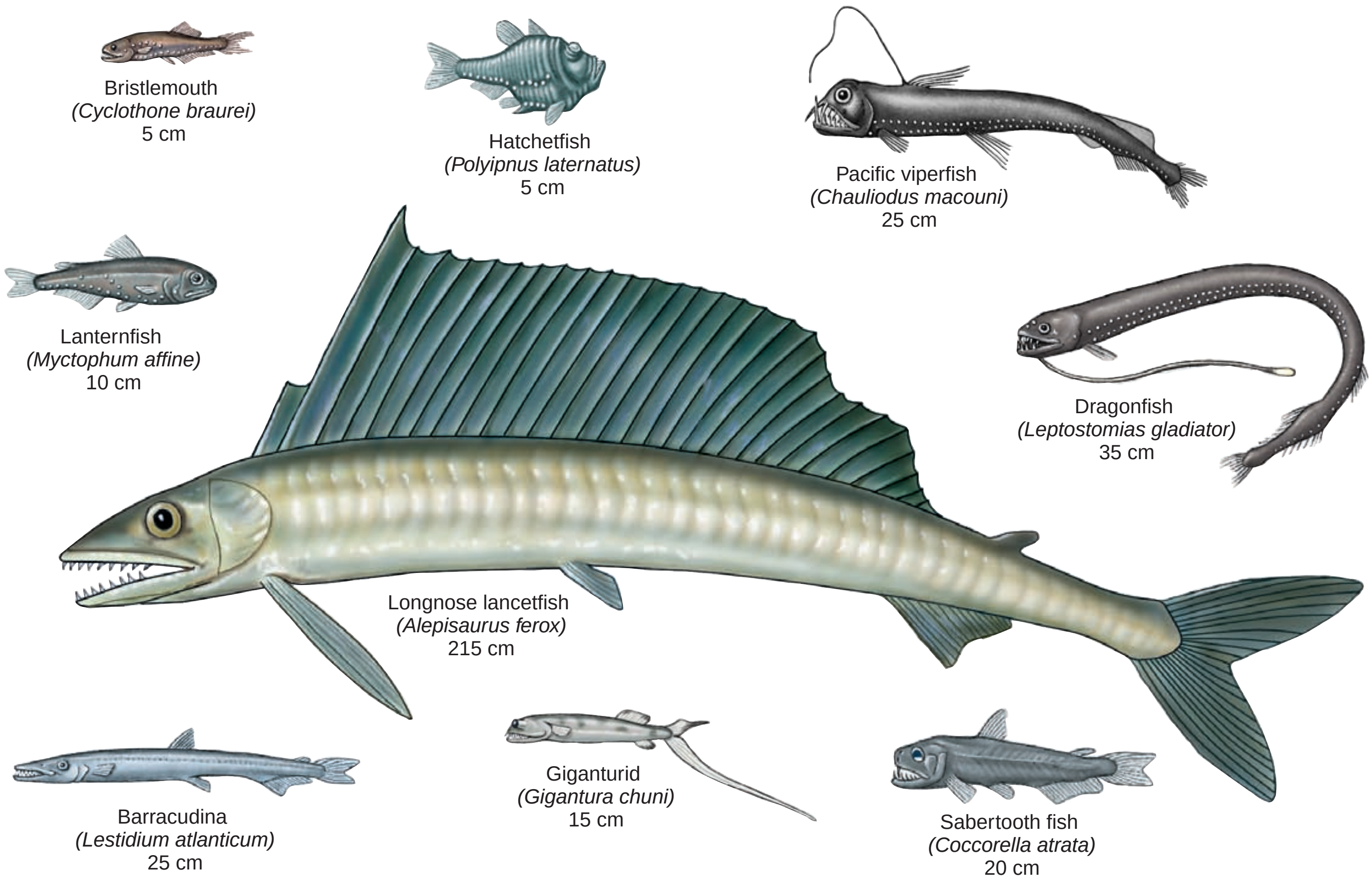
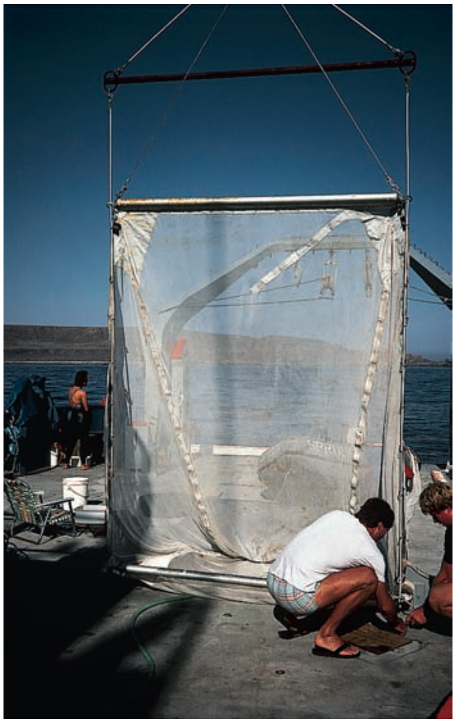

Bristlemouth
(Cyclothone braurei)
5 cm
Hatchetfish
(Polyipnus laternatus)
5 cm
Pacific viperfish
(Chauliodus macouni)
25 cm
Lanternfish
(Myctophum affine)
10 cm
Dragonfish
(Leptostomias gladiator)
35 cm
Longnose lancetfish
(Alepisaurus ferox)
215 cm
Barracudina
(Lestidium atlanticum)
25 cm
Giganturid
(Gigantura chuni)
15 cm
Sabertooth fish
(Coccorella atrata)
20 cm

FIGURE 16.6 Some typical mesopelagic fishes and their approximate maximum length.


(a)

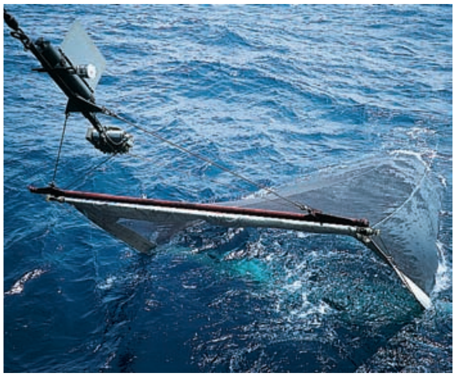

(b)

FIGURE 16.7 Nets called rectangular midwater trawls are commonly used to collect mesopelagic organisms. The net can be opened and closed by remote control when it is at the desired depth. This prevents surface organisms from being caught while the net is being lowered and retrieved. In both (*a*) and (*b*) the mouth of the net is open.

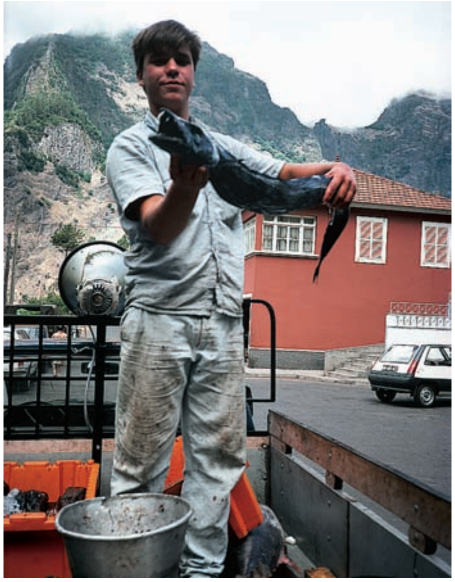


FIGURE 16.8 A black scabbard fish (*Aphanopus carbo*) being sold by a Madeiran fisherman. The fish, known locally as *espada,* is a relatively rare example of a midwater fish that is caught for food. More and more mesopelagic fishes are being exploited, however, because shallower fish stocks are depleted (see "Optimal Yields and Overfishing," p. 386).

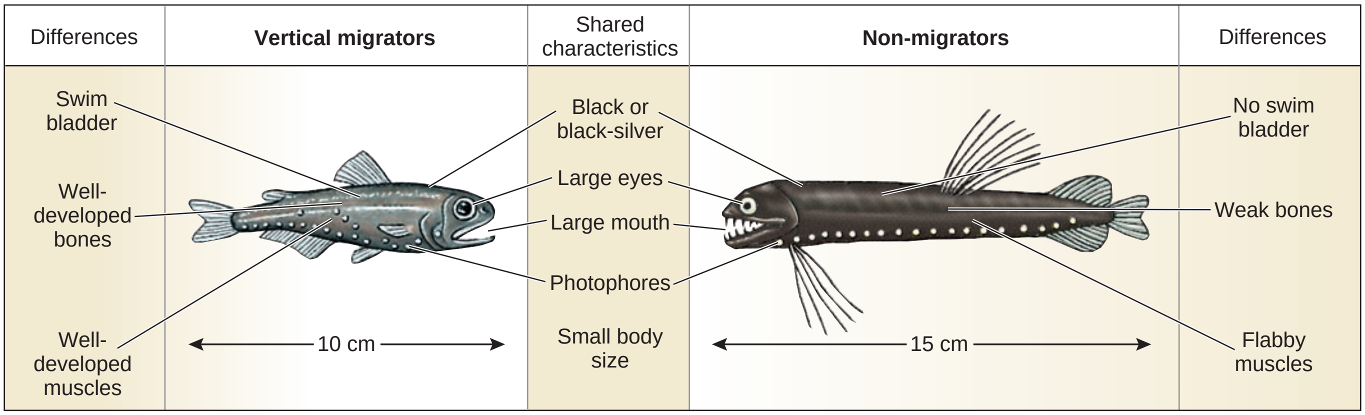


FIGURE 16.9 Some adaptations of typical mesopelagic fishes, including some differences between vertical migrators like lanternfishes (left) and non-migrators like dragonfishes (right). Compare these with the adaptations of epipelagic and deep-sea fishes shown in Figures 15.18 and 16.19.

organisms in the mesopelagic than in the epipelagic. The abundance of midwater organisms in a particular geographic area reflects the productivity of the waters above. There is more mesopelagic life under highly productive surface waters than under areas with low primary production.

Many of the characteristics of midwater animals are directly related to the lack of food in the mesopelagic. The small size of midwater fishes, for example, is thought to be an adaptation to the limited food supply. Animals need a lot of food to grow large, so there may be an evolutionary advantage to limited growth and small size.

Midwater fishes usually have large mouths, and many have hinged, extendible jaws equipped with fearsome teeth (Figs. 16.9 and 16.10). Because food is scarce below the photic zone, most fishes cannot afford to be picky. They usually have very broad diets and eat just about anything they can fit into their mouths. The large, protrusible jaws allow them to eat a wide range of prey. The advantage of this is that they don't have to pass up a potential meal because it is too large to eat. Some mesopelagic fishes can even eat prey larger than themselves! The long, sharp teeth help keep prey from escaping.

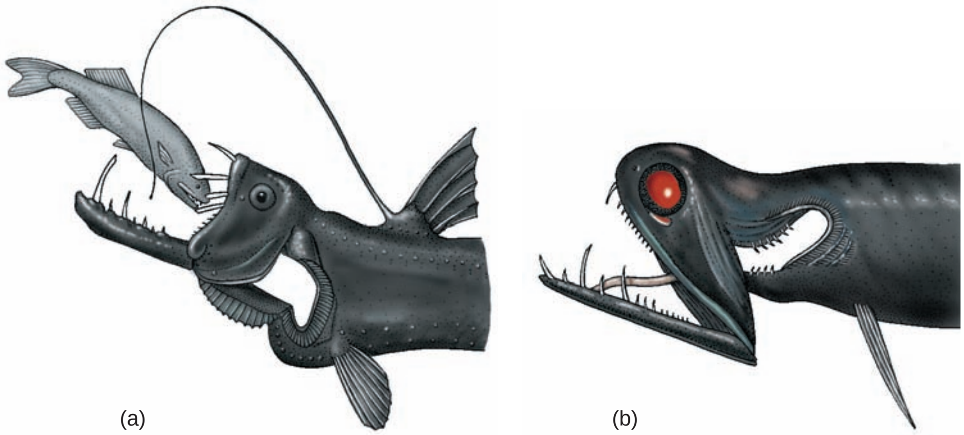


FIGURE 16.10 (*a*) The viperfish (*Chauliodus*) has hinged jaws that can accommodate large prey. (*b*) The rattrap fish (*Malacosteus*) has a similar jaw arrangement.

Common adaptations of midwater fishes include small size, large mouths, hinged and extendible jaws, needle-like teeth, and unspecialized diets. These adaptations result from the limited food supply in the mesopelagic.

Midwater animals fall into two major groups: those that stay in the mesopelagic and those that migrate to the surface at night. The non-migrators include a few species of small zooplankton, mainly copepods and krill, that filter out **detritus** and the small amount of phytoplankton that sinks out of the photic zone. The fecal pellets of epipelagic copepods and other surface grazers form an important part of the detritus eaten by mesopelagic filter feeders. Fecal pellets sink much faster than individual phytoplankton cells, so they stand a better chance of making it to the mesopelagic before being eaten.

Most non-migrating midwater animals, however, are not zooplankton but fishes, shrimps, and squids. They are sit-and-wait predators that lurk in the dim light, gulping down anything that comes within range. With food hard to come by, these organisms are adapted to conserve energy. Instead of energy-consuming muscle, non-migrating midwater fishes have flabby, watery flesh. To fill their **swim bladder** fishes must produce a gas pressure inside the bladder that matches the external water pressure. Because water pressure is greater at depth than at the surface, filling the swim bladder requires more energy in the mesopelagic. As a result, most non-migrating midwater fishes have lost the swim bladder. To compensate for the loss of the swim bladder they have evolved soft, weak

Detritus Particles of dead organic matter.
- Chapter 10, p. 223

Swim Bladder A gas-filled sac in the body cavity of most bony fishes that helps them control their buoyancy.
- Chapter 8, p. 157; Figure 8.12

bones and lost defensive structures like spines and scales. These adaptations reduce weight and make them more neutrally buoyant, allowing them to float at a constant depth without wasting energy swimming. Since they don't swim much, they have little need for the streamlining that is so characteristic of epipelagic fishes.

Vertical Migration and the Deep Scattering Layer Instead of staying put and waiting for food to fall from above, most mesopelagic organisms make **vertical migrations.** They swim up at night to feed in the rich surface layers and descend during the day to depths of several hundred meters or more. In the dim light they are probably relatively safe from predators. Some vertical migrators spend the day in a lethargic stupor, conserving energy until their next foray to the surface. Vertical migration is also seen in many zooplankton that live in the deeper parts of the epipelagic (see "Vertical Migration," p. 342).

Vertically migrating fishes differ in several important ways from those that stay in the mesopelagic (Fig. 16.9). Well-developed muscles and bones are needed to make the daily swim up and down the water column. These structures increase the weight of the fish, so these fishes have retained the swim bladder for buoyancy. As they move up and down, they experience dramatic changes in pressure. Some vertically migrating fishes can rapidly adjust the volume of gas in the swim bladder to prevent it from collapsing or exploding when they change depth. Many, however, have a swim bladder that is filled with fat instead of gas. Fat, unlike gas, does not expand and contract with pressure changes, making it much easier for the fishes to regulate their buoyancy. Vertically migrating fishes are also able to tolerate the temperature changes they experience as they move up and down across the thermocline.

Midwater animals that make vertical migrations have well-developed bones and muscles, wide temperature tolerances, and, in fishes, swim bladders. Non-migratory midwater fishes have soft bones and flabby muscles, and lack swim bladders.

Vertical migration by mesopelagic animals was discovered during World War II, when sonar came into use. Sonar soundings regularly showed a series of sound-reflecting layers, or "false bottoms." The real bottom gives a sharp, clear echo, but these layers, collectively dubbed the **deep scattering layer (DSL),** give a soft, diffuse echo that makes a shadowy trace on sonar plots. During the day the DSL lies at depths of 300 to 500 m (1,000 to 1,600 ft), but at sunset it rises to the surface. The depth of the DSL is clearly related to light intensity: The DSL stays deeper when there is a full moon than on moonless nights and even moves up and down when clouds pass over the moon.

Net tows have shown that the DSL is composed of fishes—especially lanternfishes—krill, shrimps, copepods, jellyfishes, squids, and other midwater animals. Most of these organisms, though they are found within the DSL, do not contribute to its sound-reflecting properties. Because organisms are made mostly of water, sound passes through them much as it does through seawater, without bouncing off. Air pockets, however, reflect sound quite strongly. The echo of the DSL comes mostly from sound waves bouncing off the gas-filled swim bladders of some vertically migrating fishes.

The deep scattering layer (DSL) is a sound-reflecting layer made up of vertically migrating midwater animals. Lanternfishes, krill, shrimps, copepods, jellyfishes, and squids are the dominant organisms of the DSL.

When lanternfishes, krill, and other animals return to the mesopelagic after stuffing themselves near the surface, they carry the products of surface production down with them. Thus, vertical migration greatly increases the food supply in the mesopelagic. Many non-migratory midwater predators feed heavily on vertically migrating species. Since migrators are more muscular than non-migrators, they provide a more nutritious meal.

Sense Organs To help them see in the dim light, midwater fishes characteristically have eyes that are not only large but unusually sensitive. Large, light-sensitive eyes also occur in squids, shrimps, and other groups. Some midwater fishes have developed **tubular eyes** (Fig. 16.11), a complex visual system that is almost like having two pairs of eyes. Tubular eyes give very acute vision in the direction that the eyes are pointed, either upward or forward, but are not good for lateral vision. To compensate, the **retina,** the light-sensitive part of the eye, extends partway up one side of the eye (Fig. 16.12*a*). This allows the fish to see to the side and below (Fig. 16.13). In normal fish eyes the retina lies only at the back of the eye.

Adaptations very similar to tubular eyes are found in at least one octopus (*Amphitretus;* Fig. 16.12*a*) and in the bilobed eyes of some krill (*Stylocheiron;* Figs. 16.12*c* and 16.14). One squid, *Histioteuthis,* has taken a different path to the same apparent end. One eye in these squids is much larger than the other. The squid floats in the water column with the large eye pointed upward and the small eye downward.

Many midwater animals have evolved large, light-sensitive eyes that provide good vision in dim light. Other adaptations include tubular eyes in fishes and bilobed eyes in krill.

Coloration and Body Shape Like their epipelagic counterparts, mesopelagic predators rely heavily on vision. Because midwater prey cannot afford the energetic costs of fast swimming or heavy defensive spines and scales, camouflage is perhaps even more important than in the epipelagic. The basic strategies, however, are very similar: **countershading,** transparency, and reduction of the silhouette. There are many variations on these basic strategies, especially in relation to depth and light levels.

Transparency is particularly common in the shallower and better-lit parts of the mesopelagic. Copepods, jellyfishes, shrimps,

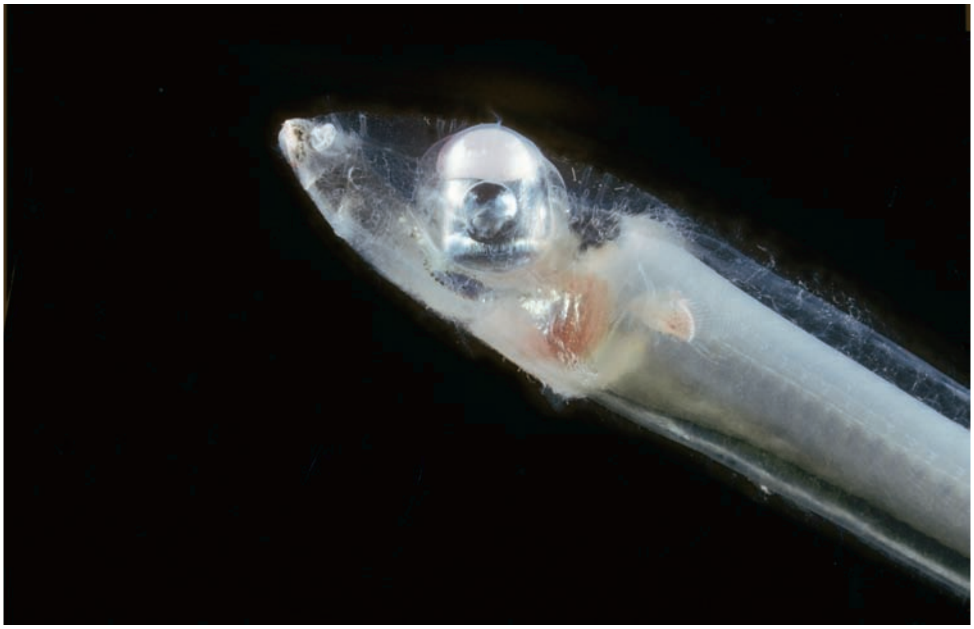


FIGURE 16.11 Many midwater fishes, like this barreleye (*Dolichopteryx longipes*), have tubular eyes that give them very acute upward vision. The large white lens at the top of the eye is very effective at gathering the dim light in the mesopelagic. This species has a second lens on the side of the eye, visible as a dark disk, that provides peripheral vision. In some species the tubular eyes point forward.

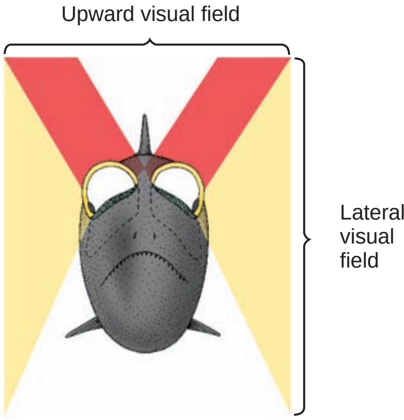


FIGURE 16.13 The field of vision of a midwater fish (*Scopelarchus*). The fish has two main visual fields corresponding to the two parts of the retina shown in Figure 16.12a.

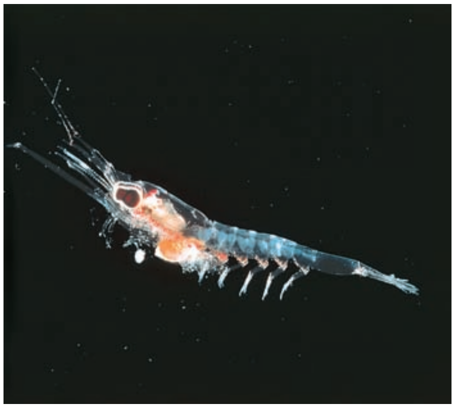
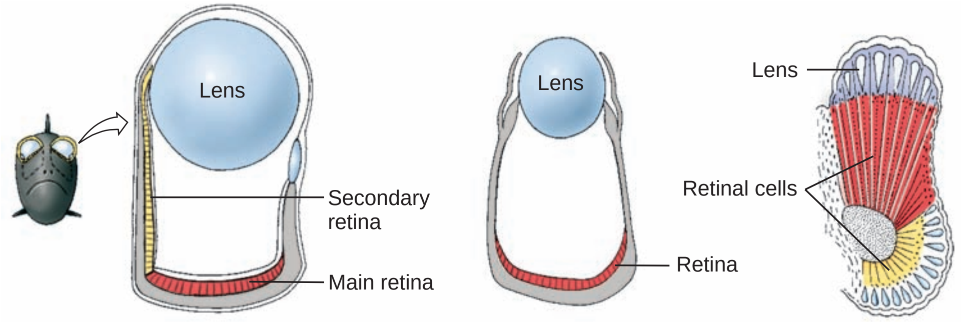


FIGURE 16.14 A midwater krill (*Nematoscelis difficilis*) with bilobed eyes.



(a) Fish (b) Deep-sea octopus (c) Krill (bilobed eye)

FIGURE 16.12 (*a*) The tubular eye of a midwater fish (*Scopelarchus*). The retina is the part of the eye sensitive to light. The part of the retina at the bottom of the eye, colored red in the diagram, provides good upward vision. The part extending up the side of the eye, colored yellow, provides lateral vision (see Fig. 16.13), which is less acute. Eyes with a similar structure have evolved in (*b*) octopuses (*Amphitretus pelagicus*) and (*c*) krill (*Stylocheiron suhmii*).

bristlemouths, and other animals that live in the upper mesopelagic tend to be transparent, some almost completely so. Deeper in the mesopelagic, fishes tend to be more silvery, and in the deepest, darkest part, black or red. Zooplankton from the deeper mesopelagic are often red, orange, or purple. These colors might be quite conspicuous at the surface, but colors change underwater (see "Transparency," p. 47). Our eyes see a fish as red at the surface because its skin absorbs most of the colors in sunlight but reflects the red. Red light doesn't penetrate to mesopelagic depths, however, and the red pigment absorbs the blue light that does, so the organism appears dark against the dark background of the surrounding water.

Mesopelagic fishes often have black backs and silvery sides, reminiscent of the countershading of epipelagic animals (see "Coloration and Camouflage," p. 340). In the mesopelagic, however, there is not enough light to reflect off the white or silver belly typical of epipelagic countershading to mask the animal's outline. Even a white object produces a silhouette in twilight. A silhouette makes the animal conspicuous and vulnerable to all those sharp eyes peering up from the depths. To reduce their silhouettes, some mesopelagic fishes, like hatchetfishes, have laterally compressed bodies. This reduces the size of the body outline whether the animal is viewed from above or below.

Bioluminescence Most midwater animals have evolved an even more effective way to mask their silhouettes. Their bioluminescent photophores, found mostly on their undersides, produce light that breaks up the silhouette and helps the animal

Countershading A pattern of coloration common in open-water nekton in which the back is black or dark blue and the underside white or silver.
- Chapter 15, p. 340

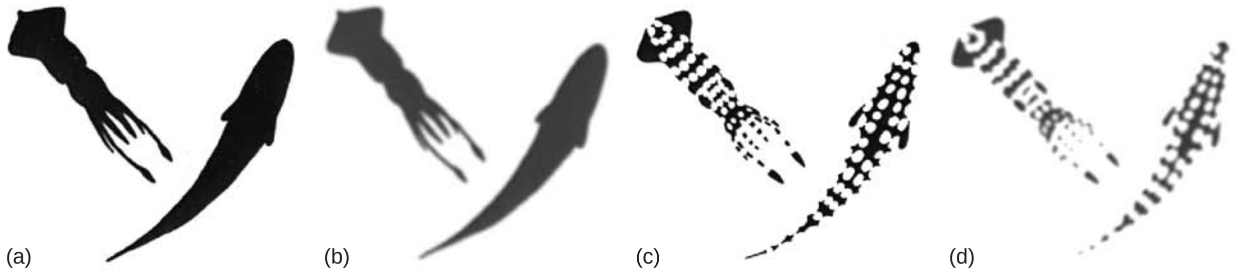


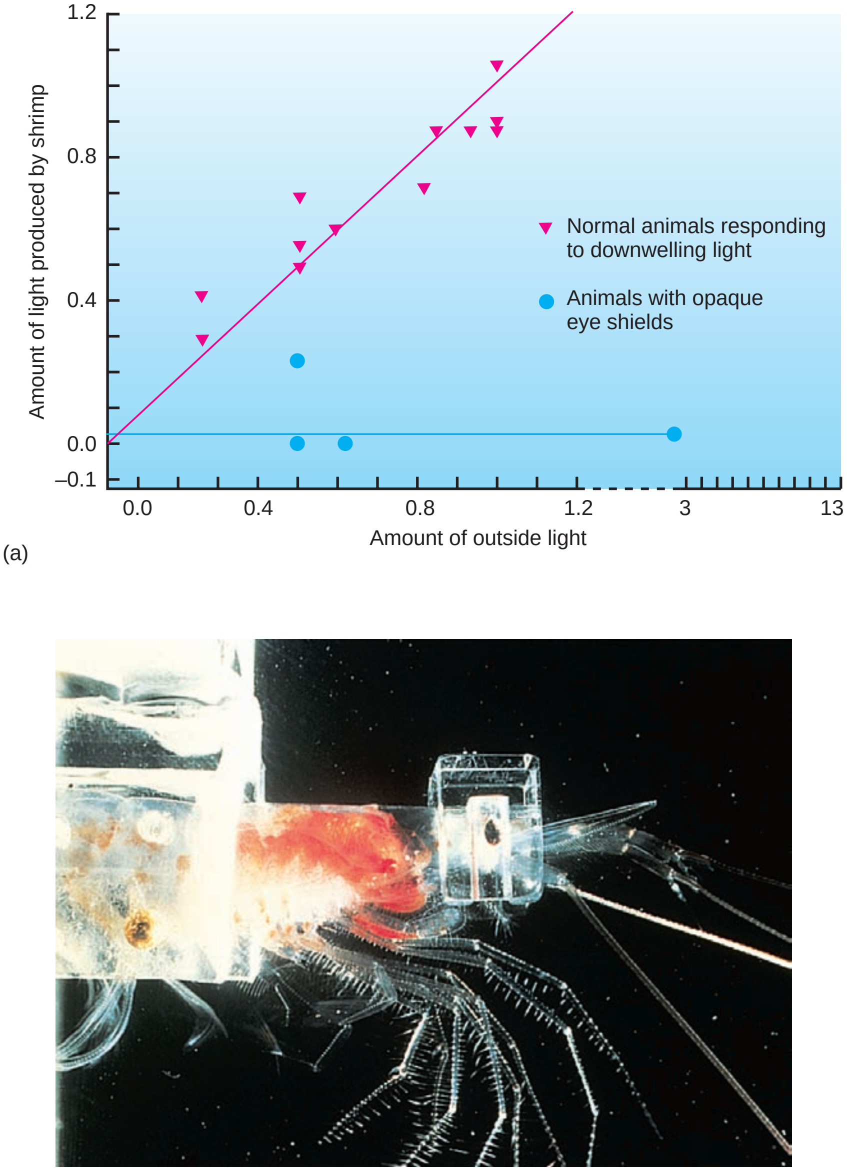
FIGURE 16.15 The value of having photophores on the lower, or ventral, surface of midwater animals is shown in this simple demonstration. (*a* and *b*) Silhouettes of two midwater organisms as they would appear without photophores. (*c* and *d*) The same animals with the photophores in white to match the background. The photophores break up the silhouette, making the animal much less visible. This effect is more pronounced when the animals are a little out of focus (*b* and *d*), as they are when viewed through the water.

blend in with the background light filtering down from the surface (Fig. 16.15). This adaptation, which functions in a similar manner to countershading, is called **counterillumination.**

The light produced by midwater animals is closely matched to the background light. Like the natural light at these depths, nearly all midwater bioluminescence is blue-green. Furthermore, many mesopelagic animals can control the brightness of the light they produce to match the brightness of the background. This has been shown experimentally by placing special blinders on shrimps and other animals. The blinders allow experimenters to control how much light the animal sees (Fig. 16.16). When the animal is exposed to bright light, it produces bright bioluminescence; when the light is dim, so is the bioluminescence. When opaque blinders are put on the shrimp so that it sees no light, it turns off its photophores completely. This control of the bioluminescence is essential. It is easy to see an animal if it produces light at night or if the light is brighter than the background. On the other hand, the animal creates a silhouette if the light isn't bright enough.

Midwater organisms have evolved ways to defeat counterillumination. The bioluminescence of most mesopelagic organisms nearly matches the color of natural light coming from above, but is just a bit greener. Some fishes have visual pigments that allow them to distinguish subtle differences among colors in the blue-green range, and many others have yellow filters that serve the same purpose. Some midwater squids can also tell the difference between bioluminescence and natural light, but they do it by having the equivalent of polarized sunglasses rather than color discrimination—natural light in the mesopelagic and bioluminescence are polarized differently.

Most midwater animals are bioluminescent, and midwater organisms have evolved many different ways to produce light. Photophores, as we have seen, are common. In some species the light is produced by the animal's own specialized tissue. In other species,



(a)

(b)

FIGURE 16.16 (*a*) This experiment showed that a midwater shrimp (*Sergestes similis;* Fig. 16.2) produces bioluminescence to match the background light intensity. Shrimp having both eyes covered with blinders did not produce any light (lower line), no matter how much outside light there was. Those with clear blinders produced more light as the outside level was increased (upper line). (*b*) The experimental setup, in this case using a control shrimp with clear blinders.

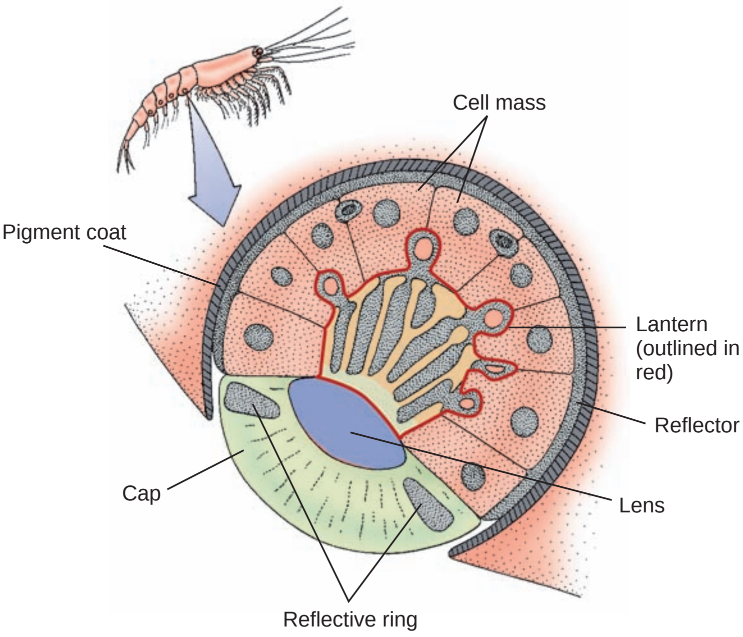


FIGURE 16.17 Cross section of a krill photophore.

symbiotic bacteria live inside the light organ and produce the light. In either case, the photophore can be quite complex (Fig. 16.17).

Bioluminescence is not always produced by specialized photophores. Many jellyfishes and other gelatinous animals produce light with cells that are scattered over the body surface. Some copepods, ostracods, shrimps, and other animals secrete bioluminescent fluids that they squirt out through special glands, either in addition to or instead of having photophores. Some squids and octopuses even produce bioluminescent ink.

Counterillumination is an important function of bioluminescence in midwater organisms, but not the only one. The pattern of photophores is different among species, and even between sexes, which may mean that bioluminescence is used to communicate and attract mates. Organisms that produce bioluminescent secretions may do so as a defense mechanism in the same way that shallow-water squids and octopuses use their ink. When disturbed, they often produce a burst of light and dart away. This presumably distracts predators and allows the prey to escape. Some animals use light to lure prey. Some have light organs around their eyes that may help them see. In fact, photophores under the eyes of a few species of midwater fishes produce red light. The red light is invisible to most other midwater organisms, but these fishes can see it and probably use it to spy undetected on potential prey.

Most midwater animals are bioluminescent. Bioluminescence is used in counterillumination to mask the silhouette, to escape from predators, to attract or see prey, and perhaps in communication and courtship.

The Oxygen Minimum Zone In many places, midwater organisms have to deal with a shortage of oxygen in the water. Oxygen enters the ocean in two ways: by gas exchange with the atmosphere (see "Dissolved Gases," p. 47) and as a by-product of photosynthesis. Once a water mass leaves the surface and descends to mesopelagic depths, there is no way for it to gain oxygen. It is removed from contact with the atmosphere, and there is not enough light for photosynthesis. **Respiration** by decay bacteria, however, continues to use up oxygen (Fig. 16.18). As a result the water becomes depleted in oxygen, often in a fairly well-defined layer around 500 m (1,600 ft) deep known as the **oxygen minimum zone (OMZ).** The amount of oxygen in the OMZ can drop to practically nothing. Below the OMZ there is very little food and therefore very little respiration and decomposition, so oxygen is not used up so quickly. Thus, the water below the OMZ retains most of the oxygen it had when it left the surface.

Animals live in the oxygen minimum zone despite the low oxygen levels. Fishes, krill, and shrimps that live there usually have large, well-developed gills to help extract what little oxygen there is. They also tend to be relatively inactive, which lowers their oxygen consumption. Many also have complex biochemical adaptations, like **hemoglobin** that functions well at low oxygen concentrations.

THE WORLD OF PERPETUAL DARKNESS

Below the mesopelagic lies the little-known world of the deep sea, where sunlight never penetrates. This alien environment is vast, indeed. It is the largest habitat on earth and contains about 75% of our planet's liquid water. The deep sea can be divided into several pelagic depth zones. The **bathypelagic zone** includes depths between 1,000 and 4,000 m (3,300 to 13,000 ft), and the **abyssopelagic zone** lies from 4,000 to 6,000 m (13,000 to 20,000 ft). The **hadopelagic,** or **hadal pelagic, zone** consists of the waters of the ocean **trenches,** from below 6,000 m to just above the sea floor, as deep as 11,000 m (36,000 ft). Each of the depth zones supports a distinct community of animals, but they also have much in common. Here we stress the similarities, rather than the differences, among the depth zones of the deep sea.

The conditions of life in the deep pelagic environment change very little. Not only is it always dark, it is always cold: The temperature remains nearly constant, typically at 1° to 2°C (35°F). Salinity and other chemical properties of the water are also remarkably uniform.

The deep sea also includes the ocean bottom beyond the continental shelf. Bottom-living organisms are covered separately (see "The Deep-Ocean Floor," p. 370).

Hemoglobin A blood protein that transports oxygen in many animals; in vertebrates it is contained in erythrocytes (red blood cells).

- Chapter 8, p. 164

Trenches Deep depressions in the sea floor that are formed when two plates collide and one sinks below the other.

- Chapter 2, p. 26; Figures 2.11 and 2.12

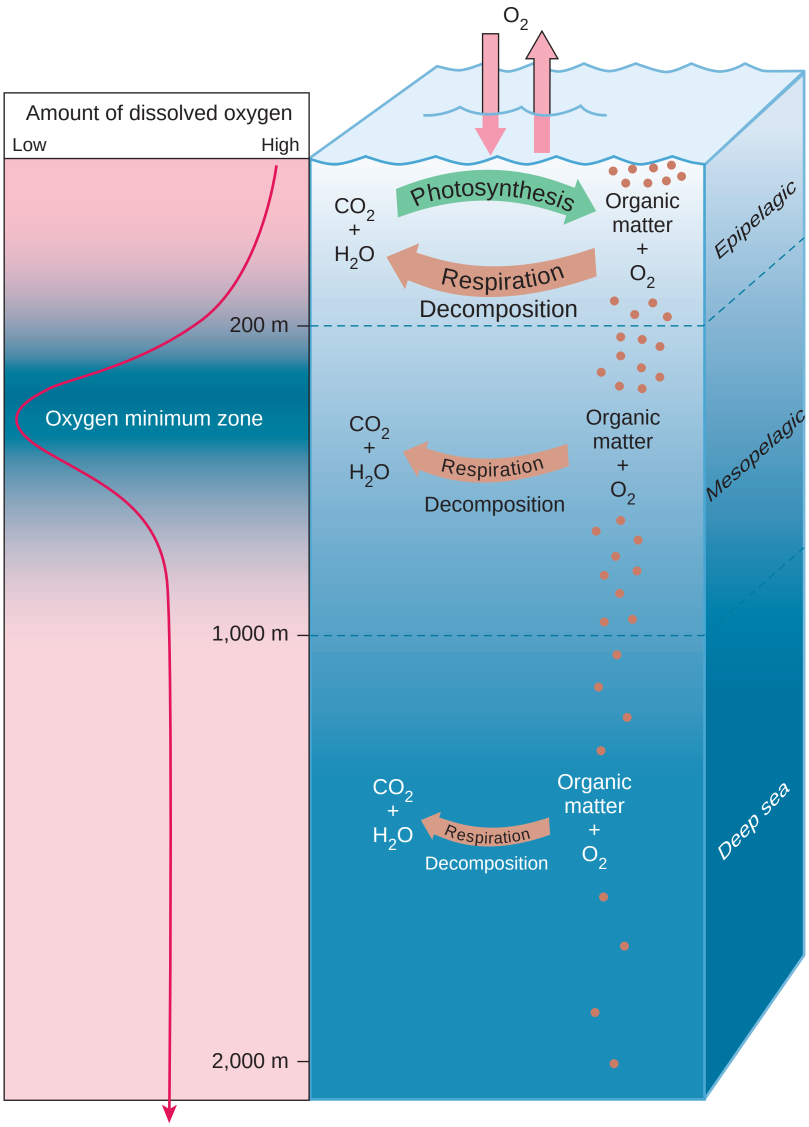


FIGURE 16.18 Surface waters are rich in oxygen, because oxygen both enters from the atmosphere and is released by photosynthesis. In the mesopelagic zone neither the atmosphere nor photosynthesis can contribute oxygen to the water, but there is extensive bacterial decomposition of organic matter sinking from shallow water. This uses up oxygen and results in an oxygen minimum zone. Below the oxygen minimum zone, most of the organic matter has already decayed on its way down, and oxygen remains dissolved in the water. Additional oxygen is brought in by the deep thermohaline circulation (see Figs. 3.24 and 3.25).

The deep sea includes the bathypelagic, from 1,000 to 4,000 m; the abyssopelagic, 4,000 to 6,000 m; and the hadopelagic, 6,000 m to the bottom of trenches. The physical environment in these zones is quite constant. The deep sea also includes the deep-sea floor.

In the darkness of the deep sea there is no need for countershading. Many animals, especially zooplankton, are a drab gray or off-white. Deep-sea fishes are generally black. Shrimps are often bright red, which in the deep sea has the same effect as being black. A few deep-sea fishes are also red.

As in mesopelagic animals, bioluminescence is very common in animals that live in the upper part of the deep sea. Deep-sea animals do not use bioluminescence for counterillumination, however, since there is no sunlight to create a silhouette. They have fewer photophores than midwater species, and the photophores are usually on the head and sides of the body rather than on the ventral surface. In the deep sea the primary uses of bioluminescence are probably prey attraction, communication, and courtship. Bioluminescence becomes less common in the deeper parts of the deep sea, for reasons that are not understood.

The large, light-sensitive eyes of midwater animals are not needed in the deep sea, where not even dim sunlight penetrates. The deep sea is not *completely* dark, however, because bioluminescence is common. Many deep-sea animals have functional eyes, especially in the upper parts of the deep sea, but the eyes are generally small (Figs. 16.19 and 16.20). Animals from the deepest regions tend to have even smaller eyes or be blind altogether. Deep-sea fishes that are blind are not bioluminescent, one indication that the major function of vision in the deep sea is to see bioluminescence.

The Lack of Food

Deep-sea organisms may not have to adapt to variations in the physical environment, but they face a continual shortage of food. Very little, only about 5%, of the food produced in the photic zone makes it past all the hungry mouths in the waters above to reach the deep sea. Deep-sea animals do not make vertical migrations to the rich surface waters, probably because the surface is too far away and the change in pressure too great. With food critically scarce, deep-sea animals are few and far between.

Deep-sea fishes, the most common of which are bristlemouths and anglerfishes (Fig. 16.21), are relatively small, generally 50 cm (20 in) or less, but on average they are larger than mesopelagic fishes. It is somewhat surprising that deep-sea pelagic fishes tend to be larger than mesopelagic ones, since there is even less food available in the deep sea than in the mesopelagic. It is thought that deep-sea fishes put their energy into growth, reproducing slowly and late in life, while mesopelagic fishes spend less energy on growth and more on reproduction. In addition, vertically migrating mesopelagic fishes expend a lot of energy in their migrations, reducing the energy available for growth.

The energy-saving adaptations to food shortage seen in midwater organisms are accentuated in the deep sea. Deep-sea fishes are sluggish and sedentary, even more so than midwater fishes. They have flabby, watery muscles, weak skeletons, no scales, and poorly developed respiratory, circulatory, and nervous systems. Nearly all lack functional swim bladders. It appears that these fishes hang in the water column, expending as little energy as possible, until a meal comes along. Most deep-sea fishes have huge mouths and can consume prey much larger than themselves. This trend reaches its peak in the swallowers (*Saccopharynx;*

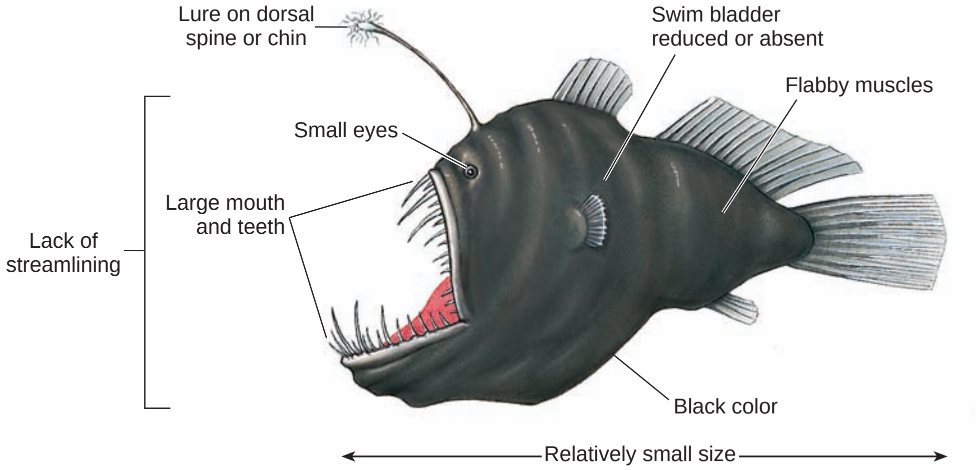


FIGURE 16.19 Some typical characteristics of deep-sea pelagic fishes. Compare these with the adaptations shown in Figures 15.18 and 16.9.

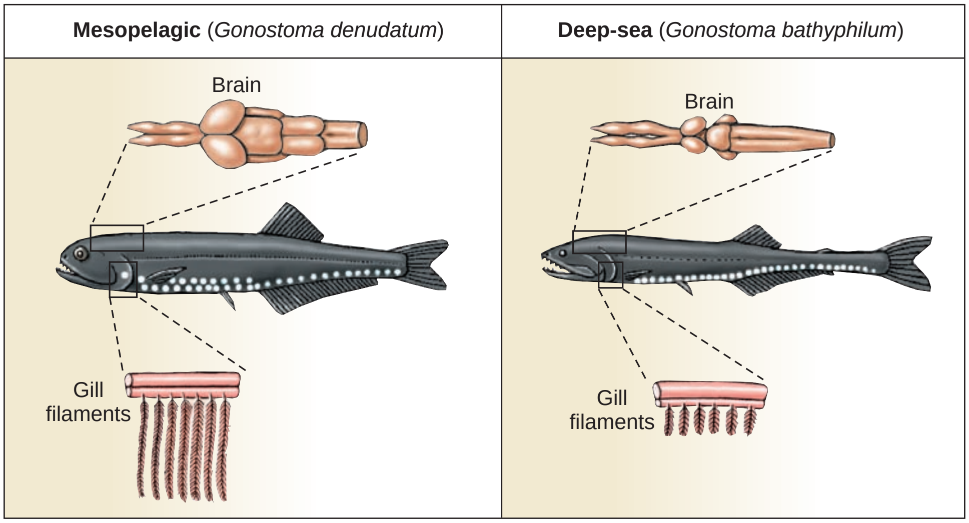

Mesopelagic (Gonostoma denudatum)
Deep-sea (Gonostoma bathyphilum)
Brain
Gill filaments
Brain
Gill filaments

FIGURE 16.20 Comparison of typical adaptations in mesopelagic and deep-sea pelagic fishes. Shown are closely related bristlemouths from the mesopelagic (*Gonostoma denudatum*) and the deep sea (*G. bathyphilum*). The deep-sea fish has smaller eyes, less muscle, and fewer light organs. It also has less-developed nervous and circulatory systems, as indicated by the smaller brain and gill filaments.

Figs. 16.21 and 16.22) and gulpers (*Eurypharynx;* Fig. 16.21), which look like swimming mouths. To go along with their large mouths, many species have stomachs that can expand to accommodate the prey once it has been engulfed.

Deep-sea pelagic fishes are typically small and black, with small eyes, large mouths, expandable stomachs, flabby muscles, weak bones, and poorly developed swim bladders. Bristlemouths and anglerfishes are the most common.

Anglerfishes have evolved an unusual method of catching food, from which they get their name. The first spine of their dorsal fin is modified into a long, movable "pole" that they wave in front of their mouths (Figs. 16.19 and 16.21). Dangling from the end of the pole is the bait, a fleshy bit of tissue that resembles a tasty meal. Symbiotic bioluminescent bacteria live in the bait, so it glows enticingly in the dark. The anglerfish gobbles down any unsuspecting victim that comes to the bait. In most species of deep-sea anglerfishes only the females have a pole and bait. Many other deep-sea fishes also attract prey with lures, often on barbels attached to the chin.

Sex in the Deep Sea

Food is not the only thing that is scarce in the deep sea. In such a vast, sparsely populated world, finding a mate can be difficult—even harder than finding food. After all, most deep-sea animals are adapted to eat just about anything they can get, but a mate has to be both the right species and the opposite sex!

Many deep-sea fishes have solved the latter problem by becoming **hermaphrodites.** After all, it would accomplish nothing if two members of the same species finally got together but were both the same sex. If every individual can produce both eggs and sperm, the ability to breed is guaranteed.

Deep-sea animals have probably also evolved ways to attract mates. Bioluminescence, for example, may send a signal that draws other members of the same species. Many species, as we have seen, have a unique pattern of light organs. Individuals may be able to recognize potential mates by the pattern. The lure of female anglerfishes differs among species, so it may have a role in attracting mates as well as prey. Chemical attraction is also important. Male anglerfishes have a very powerful sense of smell, which they use to locate females. The females apparently release a special chemical that the male can detect and follow. Such chemicals are called **pheromones.**

Some anglerfishes (*Cryptopsaras, Ceratias*) have evolved an extreme solution to the problem of finding mates. When a male locates a female, who is much larger, he bites into her side, where he remains attached for the rest of his life (Fig. 16.21). In some species the male's modified jaws fuse with the female's tissue. Their circulatory systems join, and the female ends up nourishing the male. This arrangement, sometimes called **male parasitism,** ensures that the male is always available to fertilize the female's eggs.

Hermaphrodites Individuals with both male and female gonads.
- Chapter 7, p. 117

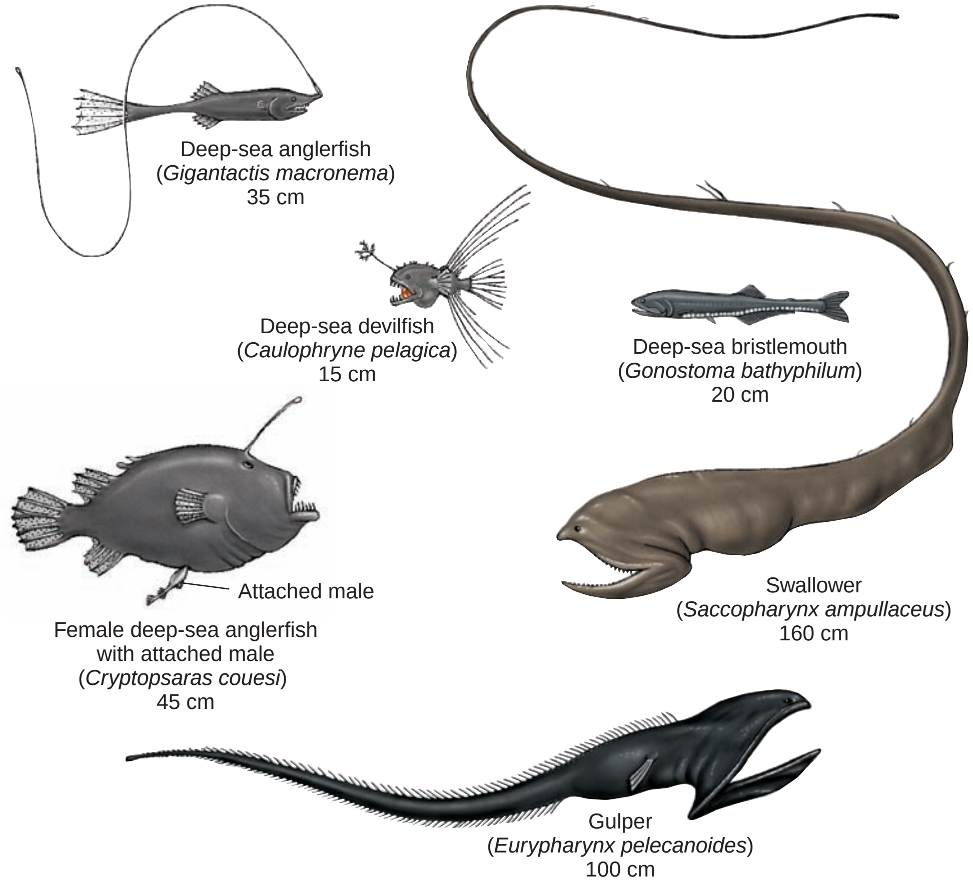


FIGURE 16.21 Some deep-sea fishes and their approximate maximum length.

Neither hermaphroditism nor male parasitism seem to be common in deep-sea invertebrates. The mechanisms that bring males and females together, if any, are unknown. There is evidence that some groups aggregate to breed, perhaps attracted by bioluminescent signals.

Finding mates, a problem for deep-sea animals, is eased by the use of bioluminescent and chemical signals and by the development of hermaphroditism and male parasitism.

Living under Pressure

Under the weight of the overlying water column, the pressure in the deep sea is tremendous. This is one reason that so little is known about the deep sea. The instruments, camera housings, and submersibles needed to study the deep sea must withstand the pressure without being crushed and are very expensive. Only a very few submersibles can venture into the deepest trenches, where the pressure may exceed 1,000 atmospheres (14,700 psi). It is just as difficult to bring animals up from the deep sea as it is for us to go down to them. Unable to endure the enormous change in pressure, they usually die when brought to the surface. A few scientists have succeeded in retrieving organisms from the deep sea in special pressurized chambers. Much has been learned from such work, but it is frustratingly difficult.

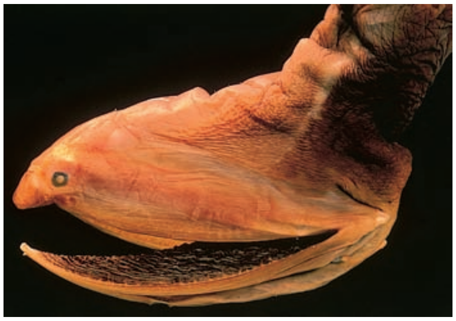


FIGURE 16.22 The gigantic mouth and jaws of the swallower eel (*Saccopharynx*) allow it to take advantage of infrequent, large meals.

It is clear that pressure has important effects on deep-sea organisms. The absence of a functional swim bladder in most deep-sea fishes, for example, is probably due to the high energetic cost of filling the bladder with gas under extreme pressure. Along with the availability of food, pressure seems to be a major factor causing zonation in deep-sea pelagic organisms, that is, dividing the deep sea into bathypelagic, abyssopelagic, and hadopelagic zones.

In shallow-water organisms the **enzymes** that control **metabolism** are strongly affected by pressure, and would cease to function at the pressures of the deep sea. Deep-sea organisms, however, have much more pressure-resistant enzymes. Some also have high concentrations of a chemical that helps to stabilize the enzymes. Such molecular adaptations enable deep-sea organisms to survive under pressures that would kill any surface-dweller.

Nonetheless, pressure probably limits the depth range of most organisms, and the number of species declines going deeper and deeper. The deepest known fish was recorded at a depth of 8,370 m (27,460 ft). Invertebrates, however, have been found in the Mariana Trench, the deepest part of the ocean.

Hydrostatic pressure is great in the deep sea and partially controls the depth distribution of deep-sea organisms. Deep-sea organisms have molecular adaptations that allow their enzymes to function at high pressure.

THE DEEP-OCEAN FLOOR

The floor of the deep sea shares many characteristics with the pelagic waters immediately above: the absence of sunlight, constant low temperature, and great hydrostatic pressure. Nevertheless, the biological communities of the deep-sea floor are very different from pelagic communities because of one key factor: the presence of the bottom.

Marine biologists have learned a bit more about the **benthos,** or bottom-inhabiting organisms, of the deep sea than about deep-water pelagic communities, but much is still unknown. Of the 270 million km^2 (105 million mi^2) of deep-sea floor, only about 500 m^2 (5,400 ft^2), the floor area of a large house, have been quantitatively sampled. What we do know has been learned using a variety of techniques. Devices called epibenthic sleds are dragged along the bottom, scooping up organisms, and corers actually bring a chunk of the bottom to the surface. Deep-sea cameras are used to photograph fast-swimming animals like fishes that are hard to catch in nets. Scientists have even developed a miniature transmitter that can be hidden in bait and used to track the movements of a fish that swallows it. Deep submersibles like *Alvin* (see Fig. 1.10) have also been very useful, even more so than in the water column. Remote-controlled robots (Fig. 16.23) are used to collect samples, take photos, and perform experiments. In 1995 one such craft succeeded for the first time in reaching the deepest part of the ocean. The Japanese-built *Kaiko* descended 10,991 meters (36,061 ft) to the floor of the Challenger Deep in the Mariana Trench. This broke the long-standing record of the submersible *Trieste,* which in 1960 descended to 10,919 meters (35,810 ft), also in the Mariana Trench.

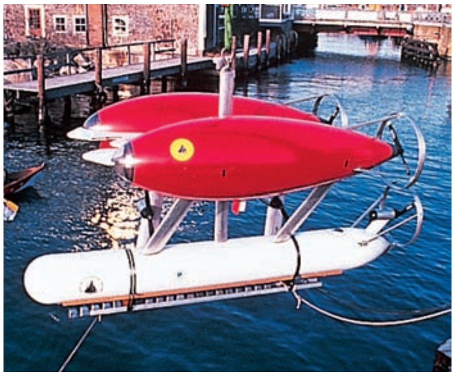


FIGURE 16.23 *ABE (Autonomous Benthic Explorer)* is an autonomous underwater vehicle—a submarine robot that functions completely independently, with no cable or wires to the surface. *ABE* is designed to spend long periods on the sea floor, inactive most of the time but "waking up" at regular intervals to cruise over a predefined track on the sea floor, taking videos and making measurements. On an acoustic signal from a ship, *ABE* floats to the surface to download its information and recharge its batteries before going back to work in the ocean depths.

Feeding in the Deep-Sea Benthos

Food shortage is critical on the floor of the deep sea. Very little of the surface production makes it all the way to the bottom. Benthic organisms, however, have a major advantage over the deep-sea pelagic ones above. In the water column, food particles that are not immediately located and eaten sink away and are lost. Once food reaches the bottom, by contrast, it stays put until it is found. Thus, although pelagic animals may get first crack at food sinking out of the photic zone, benthic animals have more time to find and eat it. Food particles that reach the bottom tend to be those that sink fairly rapidly, minimizing the chance that they will be eaten on the way down. Fecal pellets, for example, are an important source of organic matter for the deep-sea benthos.

Still, the rain of organic matter to the sea floor is actually more like a drizzle. Very little food is available to the benthic community. Furthermore, much of the material that reaches the sea floor, like the chitinous remains of crustacean zooplankton, is not immediately digestible. On the sea floor, however, bacteria decompose the **chitin** and become food for other organisms.

Most of the deep-sea floor is covered in fine, muddy sediment. The **meiofauna,** tiny animals that live among the sediment particles (see "Life in Mud and Sand," p. 291), are the most abundant organisms on the deep-sea floor, typically outnumbering larger organisms by a factor of 10. The meiofauna graze on bacteria and absorb dissolved organic matter (DOM) from the water between the sediment grains. The energy in the bacteria and DOM is thus made available to larger animals, or **macrofauna,** that graze on the meiofauna.

Suspension feeders are rare among the larger organisms in the deep-sea benthos. Instead, **deposit feeders** dominate. Many of these are **infauna,** burrowing in the sediments. Others, the **epifauna,** rest on the sediment surface.

Polychaete worms are usually the most abundant macrofauna on the deep-sea floor, followed by crustaceans and bivalve molluscs, but there is considerable variation from place to place. Sea cucumbers are sometimes dominant, for example. Sea cucumbers from the deep sea often have strange, highly modified body forms. Some have leg-like appendages and walk across the bottom in search of organic-rich sediment (see the photo on p. 357). "Herds" of some species have been observed from submersibles. Other species can swim above the sea floor by undulating their bodies or squirting jets of water. Some parts of the deep sea are dominated by brittle stars, and sea stars can also be abundant.

The deep-sea benthos is dominated by deposit feeders. The dominant animal groups are the meiofauna, polychaete worms, crustaceans, bivalve molluscs, sea cucumbers, brittle stars, and sea stars.

There are predators in the deep-sea benthos, but they seem to be fairly rare. The main predators on deposit-feeding animals are probably sea stars, brittle stars, and crabs. Members of the nekton, like fishes and squids, are also important predators. Sea spiders, or pycnogonids, prey on other invertebrates by sucking out their soft parts. Sea spiders are small in shallow water, but some deep-sea species can be as large as 80 cm (30 in) across. This reversal of the usual trend of small size in deep-sea organisms

Enzymes Proteins that speed up and control chemical reactions in organisms.
- Chapter 4, p. 65

Metabolism The vast set of chemical reactions that sustains life.
- Chapter 4, p. 64

Chitin Highly resistant carbohydrate found in the skeleton of crustaceans and other structures.
- Chapter 4, p. 65

Suspension Feeders Animals, including *filter feeders,* that eat particles suspended in the water column.
Deposit Feeders Animals that eat organic matter that settles to the bottom.
- Chapter 7, p. 116; Figure 7.3

EYE ON SCIENCE

Gelatinous Zooplankton and Carbon Flux to the Deep Sea

The importance of gelatinous zooplankton like jellyfishes, larvaceans, and salps in pelagic food webs long went unrecognized because much of their contribution is in the form of mucus that isn't readily caught in plankton nets. The *Challenger* expedition (see "The *Challenger* Expedition," p. 3) showed that dead salps can sink down to deep water, but new observations are revealing that gelatinous zooplankton may be a major source of food for deep-sea benthic communities.

Most areas of the deep-sea floor depend on the meager rain of food that originates in the sunlit surface layers far above. Much of the surface production sinks too slowly to ever reach the bottom before it decomposes or gets eaten, so the food supply is largely delivered to the bottom in relatively fast-sinking organic particles, particularly fecal pellets excreted by zooplankton, including salps and larvaceans. The flux, or rate of input, of organic carbon to the deep sea is usually measured with sediment traps designed to catch these particles, which are mostly less than 5 mm (0.2 in) in size. The traps generally miss the large, fragile particles formed by gelatinous zooplankton, such as jellyfish and salp carcasses and discarded larvacean houses (see "Non-Crustacean Zooplankton," p. 333). Technologies including submersibles, remotely operated vehicles (ROVs), and deep-sea camera systems are now allowing scientists to fill this gap.

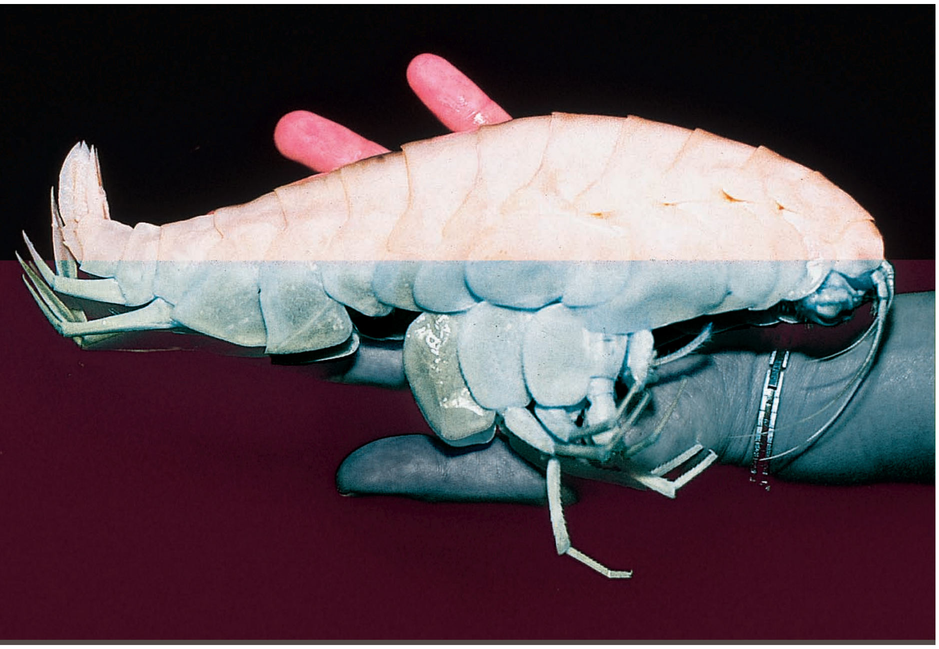
In a decade-long study in Monterey Canyon off the coast of California (a convenient place for deep-sea studies because great depths can be accessed close to shore), scientists used an ROV and video cameras to measure the abundance and sinking rate of discarded larvacean houses, and to collect them to analyze their carbon content. Their calculations indicate that larvacean houses supply as much as half of the food supply to the sea floor. Even more impressively, British biologists using remote camera sleds observed masses of dead jellyfish (*Crambionella orsini*) on the bottom of the Arabian Sea shortly after large numbers of the jellyfish were observed at the surface. The scientists estimate that the jellyfish, in one short pulse, supplied more than 10 years' worth of the normal carbon supply to the bottom in that area.

Scientists are anxious to refine their estimates of how much organic carbon gelatinous zooplankton provide to the deep-sea benthos. Expeditions planned for Monterey Canyon, for example, will measure the vertical distribution and feeding rates of salps, and the associated carbon flux. These studies look set to solve a long-standing discrepancy between the apparent energy requirements of deep-sea benthic communities and their measured food supply. By rapidly transferring large amounts of carbon into deep-sea sediments, gelatinous zooplankton may also speed the removal of carbon dioxide from the atmosphere and thus play a significant role in regulating Earth's climate (see "Our Changing Planet," p. 231).

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

is also found in other invertebrate groups, especially crustaceans (Fig. 16.24). The reasons for this phenomenon, known as **deep-sea gigantism,** are not known.

FIGURE 16.24 For unknown reasons the deep-sea members of some groups are giants compared to their shallow-water relatives. This is a deep-sea amphipod (*Alicella gigantea*).



Tripod fishes are another interesting group of deep-sea benthic predators. Nearly blind, these fishes sit on the bottom on their elongated fins (Fig. 16.25), facing into the current and snapping up passing plankton.

The slow rain of food to the bottom is interrupted by an occasional "storm." Large pieces of food that sink rapidly, like the dead bodies of large fishes or whales, are an important source of food to the benthos. Mobile deep-sea animals rapidly congregate around such "baitfalls" (Fig. 16.26). Among the most common of these are crustaceans, especially amphipods (Fig. 16.24), which arrive soon after the bait touches down. Many deep-benthic amphipods are generalists that feed on detritus and perhaps prey on live organisms if nothing else is available. Some, however, seem to specialize as scavengers. They apparently have a well-developed sense of smell, which probably helps them find new baitfalls. When caught in traps, these amphipods often have nothing in their guts except the bait, which indicates that they have not fed for some time before. This, and the fact that they have an expandable gut, may mean that the amphipods are adapted to capitalize on large but infrequent meals.

Various fishes also find freshly placed bait quickly. The most common are grenadiers, or rattails, brotulas and cusk eels, deep-sea spiny eels, and hagfishes (Fig. 16.25, also see Fig. 8.2). These bottom scavengers

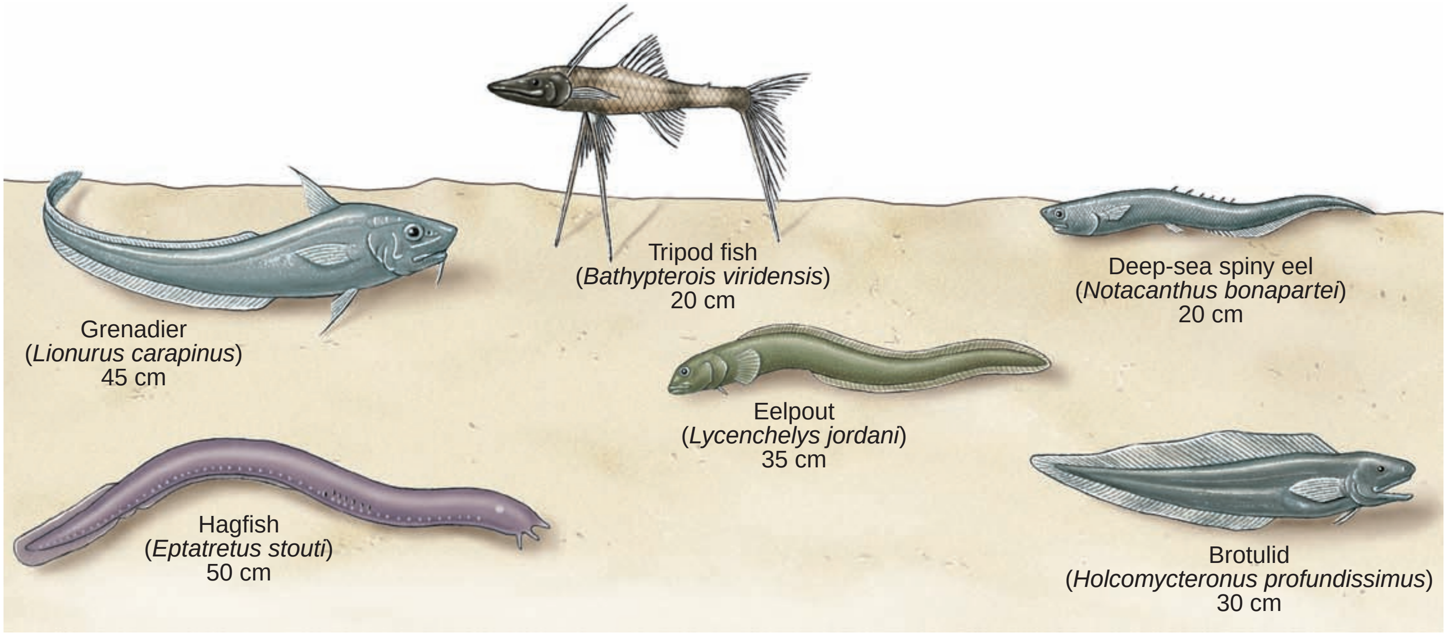


FIGURE 16.25 Some typical deep-sea bottom fishes and their approximate maximum length.

tend to be larger on average than deep-sea pelagic fishes, relatively muscular, and active, unlike bathypelagic fishes (Fig. 16.27). They seem to be adapted for cruising along the bottom in search of the occasional bonanza. In several groups the parts of the brain devoted to olfaction are highly developed compared to close relatives from the mesopelagic, where visual areas dominate. Thus, deep-sea bottom fishes, like invertebrates, probably rely a lot on their sense of smell. At depths above 2,000 m, sharks may also show up at deep-sea bait falls, quickly putting an end to the feed.

The Nature of Life in the Deep-Sea Benthos

There is a growing realization that life in the deep sea proceeds at a very different pace than it does at the surface. Most deep-sea animals seem to grow very slowly, probably because of the lack of food. On the other hand, they live for a long time. Deep-sea clams have been estimated to be 50, 60, or even 100 years old. Some fishes live even longer (see “Biodiversity in the Deep Sea,” p. 375). Perhaps the low temperature and high pressure slow down the processes of life in the deep sea.

It may also be that deep-sea animals need to live a long time to store up enough energy to reproduce. The larvae of deep-sea forms do not spend time in the food-rich photic zone. The chances of making it all the way to the surface and then back to the deep-sea floor are simply too small. Instead, deep-sea animals tend to produce large eggs, with enough yolk to see the larva through its early stages without eating. It takes a lot more energy to produce a large egg than a small one, so deep-sea animals produce only a few eggs. In at least some animals, reproduction may be tied to feeding. In some species of amphipods, individuals caught in baited traps are all sexually immature. Biologists have speculated that they do not reproduce until they manage to find a good meal.

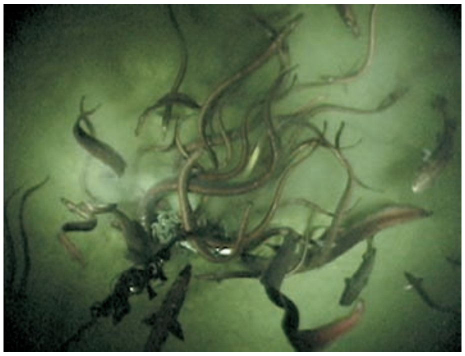


FIGURE 16.26 A variety of fishes quickly locate large pieces of food on the deep-sea floor. These cusk eels (*Genypterus blacodes*), spiny dogfish sharks (*Centrophorus squamosus*), cutthroat eels (*Diastobranchus capensis*), and snubnose eels (*Simenchelys parasiticus*) have come to a large piece of fish placed at 1,500 m (5,000 ft) on the sea floor near New Zealand.

Bacteria in the Deep Sea

Bacteria play many important roles in deep-sea benthic ecosystems that we are only beginning to understand. In 1968 a famous unplanned “experiment” gave an early indication of how much there is to learn. As the crew of *Alvin* was preparing for a dive the submersible was swamped by a wave, its supporting cable snapped, and *Alvin,* hatch open, dropped 1,540 m (5,000 ft) to the bottom. The crew escaped but left their lunch on board. It was to become the most famous lunch in marine biology.

When *Alvin* was recovered 10 months later, scientists discovered that the long-lost lunch was in amazingly good condition. Though soggy, the sandwiches looked almost fresh; the bologna was still pink inside. The rest of the lunch—apples and a thermos of soup—also looked good enough to eat. Once brought to the surface the food soon spoiled, even though it was refrigerated.

Why was the food preserved in the deep sea? Though the deep sea is cold, so is a refrigerator. Are bacteria absent from the deep sea? Does the pressure somehow

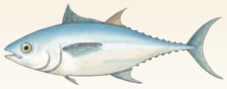
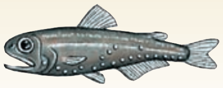
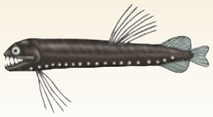
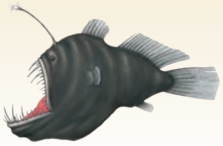
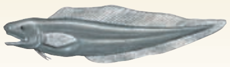
	Epipelagic	**Mesopelagic** (vertical migrators)	**Mesopelagic** (non-migrators)	**Deep pelagic**	**Deep-sea bottom**
Appearance					
Size	Wide size range, from tiny to huge	Small	Small	Relatively small, larger than mesopelagic	Relatively large
Shape	Streamlined	Relatively elongated and/or laterally compressed	Relatively elongated and/or laterally compressed	No streamlining, often globular in shape	Very elongated
Musculature	Strong muscles, fast swimming	Moderately strong muscles	Weak, flabby muscles	Weak, flabby muscles	Strong muscles
Eye characteristics	Large eyes	Very large, sensitive eyes	Very large, sensitive eyes, sometimes tubular eyes	Eyes small, sometimes absent	Small eyes
Coloration	Typical counter-shading: dark back and white or silver belly	Black or black with silver sides and belly; counterillumination	Black or black with silver sides and belly; counterillumination	Black, occasionally red, often lack coloration at greatest depths	Dark brown or black
Bioluminescence	Bioluminescence relatively uncommon	Bioluminescence common, often used for counterillumination	Bioluminescence common, often used for counterillumination	Bioluminescence common, often used to attract prey	Only a few groups bioluminescent

FIGURE 16.27 Comparison of the typical characteristics of fishes from different depth zones in the pelagic realm.

inhibit bacterial decay? Is there some other explanation? These questions sparked a flurry of research.

It is now known that bacteria do live in the deep sea, as they do in every other environment on earth. Pressure and cold slows bacterial growth, however, and most shallow-water bacteria cannot grow at the pressure and temperature of the deep sea. Therefore, the bacteria that were already in the lunch probably died when *Alvin* sank.

Even if the surface bacteria died, there are still plenty of bacteria already living in the deep sea. Deep-sea bacteria don't just tolerate the prevailing cold and high pressure, many of them grow best or even *only* under these conditions. Even though these cold-loving (psychrophilic) and pressure-loving (barophilic) bacteria grow best under deep-sea conditions, however, they still grow slower than shallow-water bacteria and can take up to 1,000 times longer to decompose organic matter. It has also been suggested that deep-sea bacteria are adapted to use organic matter in low concentrations, and are overloaded by such unusually rich fare as a bologna sandwich. Furthermore, the lunchbox may have prevented many bacteria, such as those that live on or in amphipods and other deep-sea animals, from getting to the food in the first place.

Deep-sea sediments also contain large numbers of **chemosynthetic prokaryotes,** which are probably an important food source for deposit feeders. They may be involved in the formation of polymetallic nodules and other mineral deposits (see "Ocean Mining," p. 398). Scientists have also learned that chemosynthetic bacteria are gradually digesting the wreck of the *Titanic!*

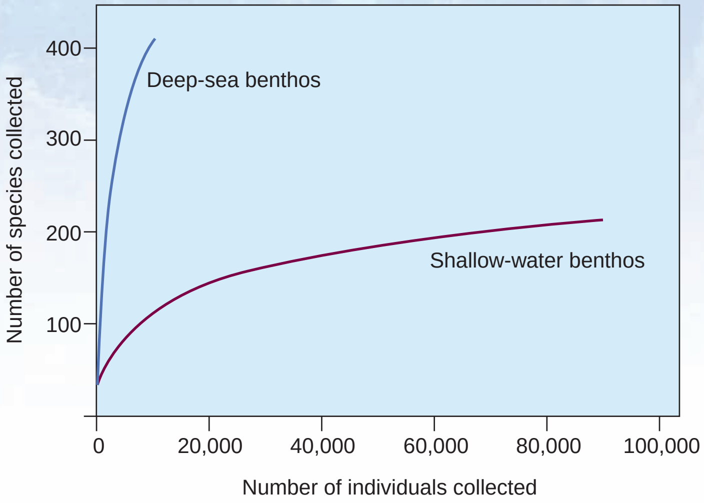
HOT SPRINGS, COLD SEEPS, AND DEAD BODIES

The year 1977 marked one of the most exciting discoveries in the history of biology, and it wasn't even made by biologists! A group of marine geologists and chemists was using *Alvin* to look for **hydrothermal vents** on a section of mid-ocean ridge near the Galápagos Islands in the Eastern Pacific. When the *Alvin* scientists found the vents, they also found something completely unexpected: a rich, flourishing community unlike anything ever imagined (Fig. 16.28). In the days that followed, more vents were found, each teeming with animals. There were gigantic worms up to 1 m (3.3 ft) long, 30-cm (12-in) clams, dense clusters of mussels, shrimps, crabs, fishes, and a variety of other unexpected life. The vents were like oases of life on the barren deep-sea floor.

Expeditions were soon mounted to hydrothermal areas around the world. With every dive, it seems, come new discoveries. Over 400 new animal species—and counting—have been found in hydrothermal vent communities, which vary considerably

Biodiversity in the Deep Sea

With its immense pressure, near-freezing waters, absence of sunlight, and chronic food shortage, the deep sea seems like one of earth's least hospitable environments. Indeed, in the nineteenth century the pioneering oceanographer William Forbes (see "The *Challenger* Expedition," p. 3), observing that fewer and fewer organisms were caught in nets as depth increased, hypothesized that no life at all existed below about 600 m (2,000 ft). This "azoic hypothesis" was quickly proved wrong when other scientists caught animals from greater depths. Nevertheless, animal abundance does decrease with depth—animals are scarce in the deep sea.



Species accumulation curves from the deep-sea and shallow-water benthos off the coast of New England.

It was once thought that in addition to low abundance there were relatively few animal species in the deep sea. Recent studies indicate that just the opposite is true: The deep sea may be the most biologically diverse environment on earth. Biologists are unable to collect and identify every species present in most environments, so they never know the exact number of species there. They can estimate species numbers, however, from "species accumulation curves." This involves analyzing how often they find new species as they collect more and more individual organisms. The first organism collected will always be a species new to the study. The second organism could be from the same species, leaving the total number of species collected at one, or it might be a new species, bringing the species total to two. If the number of species in the habitat—one measure of its **biodiversity**—is small, then as more and more individuals are collected the number of new species increases relatively slowly and soon starts to level off near the total number of species that live in the environment. In highly diverse habitats, ones with many species, the number of species increases rapidly as more individuals are collected and takes longer to level off.

When this was done on the deep-sea floor, the species curve went through the roof, leading the researchers to estimate that certainly more than 1 million, and possibly more than 10 million, species live on the deep-sea floor, making it as or more diverse than rain forests and coral reefs. This was little short of astonishing because up until then most biologists had thought that no more than a few hundred thousand species lived in the entire ocean!

The estimate of 10 million species on deep-sea floor has been controversial, in part because it is extrapolated from samples of only a tiny fraction of the sea floor. Whatever the true number, it is clear that the deep-sea floor is among the planet's most diverse habitats.

Seamounts, which like the rest of the deep sea have hardly been studied, also have very high diversity. Recent samples from only 24 seamounts in the southwest Pacific near Australia produced more than 850 species, and the species accumulation curve was still rising, indicating that many more species would have been found had more samples been taken. What is more, about a third of the species collected were new to science, and probably restricted to small seamount chains or even individual seamounts. Seamounts seem to be deep-sea islands, each holding a collection of organisms found nowhere else.

With some 30,000 seamounts in the deep sea, nearly all unexplored, there must be vast numbers of seamount species waiting to be discovered, but many may go extinct before that happens. Seamounts are home to the orange roughy (*Hoplostethus atlanticus*) and several other commercially valuable fishes. These fishes live for more than a hundred years, but take decades to reach reproductive age and reproduce very slowly, so they are vulnerable to overfishing (see "Optimal Yields and Overfishing," p. 386). A number of newly discovered populations on seamounts in the Indian Ocean, for example, were completely fished out less than three years after their exploitation began. Even worse, the bottom trawls used to catch these fish rip animals from the bottom, reducing the abundance of benthic organisms by 80% or more. With many seamounts located on the "high seas," that is, outside the jurisdiction of any country, protecting the rich biodiversity of seamounts will require an international effort to control the damage inflicted by seamount fisheries.

from place to place. Tubeworms, clams, crabs, and shrimps typically dominate the Eastern Pacific vent communities that were first discovered. Unusual snails and barnacles are most common at vents in the Western Pacific, while vents on the Mid-Atlantic Ridge are typically dominated by a shrimp (*Rimicaris*).

With no sunlight to support photosynthesis, the primary producers in hydrothermal vent communities are chemosynthetic archaea and bacteria. Around the mid-ocean ridge, seawater trickles down through cracks and fissures in the earth's crust and is heated to very high temperatures. Rich in sulfide minerals, it emerges at hydrothermal vents to form "black smokers," "chimneys," and other mineral deposits. The hot water also contains large amounts of **hydrogen sulfide** (H_2S), which is toxic to most organisms but is an energy-rich molecule. Chemosynthetic prokaryotes that use the energy in hydrogen sulfide and sulfide

Chemosynthetic Prokaryotes Autotrophic *bacteria* and *archaea* that use energy contained in inorganic chemicals rather than sunlight to make organic matter.

- Chapter 5, p. 92; Table 5.1

Hydrothermal Vents Undersea hot springs associated with mid-ocean ridges.

- Chapter 2, p. 37

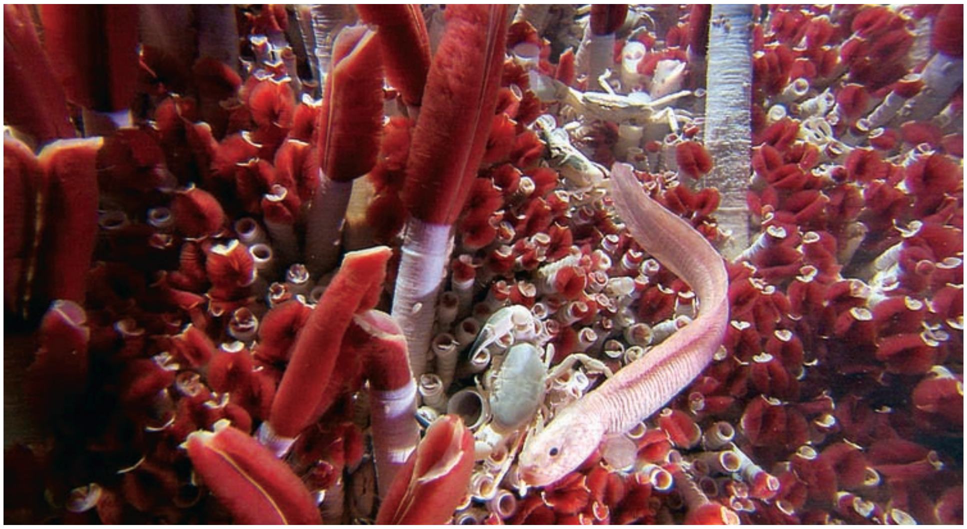


FIGURE 16.28 Rich, colorful animal communities live at many hydrothermal vents. This community at a depth of over 2,500 m (8,200 ft) on the East Pacific Rise includes giant tube worms (*Riftia*), zoarcid fish, or eelpouts, and crabs (*Bythograea*). Image courtesy of Richard A. Lutz.

minerals to make inorganic matter are the base of the food chain. Some of these microbes are extremophiles that can live at temperatures over 120°C (250°F), the highest temperature at which life is known to occur (see "Archaea," p. 89).

> Deep-sea hydrothermal vents harbor rich communities. The primary production that supports these communities comes from microbial chemosynthesis, not photosynthesis.

Water near the vents contains so many microbes that they cloud the water. Some vent animals feed by filtering them from the water, but this isn't the principal mode of feeding. One of the dominant tubeworms in Eastern Pacific vent communities (*Riftia*) does not filter-feed. In fact, it doesn't even have a mouth or digestive tract! Instead, these worms have a highly specialized organ called a trophosome ("feeding body"; Fig. 16.29), packed with symbiotic bacteria. The bacteria perform chemosynthesis inside the worm's body and pass much of the organic matter they produce on to the worm. The worm, in turn, supplies the bacteria with raw materials. The bright-red plume acts like a gill, exchanging not only carbon dioxide and oxygen, but also hydrogen sulfide. The tubeworm's blood has special hemoglobin that chemically binds the hydrogen sulfide, protecting the worm from its toxic effects, and transports it to the bacteria in the feeding body. Most other vent animals chemically process hydrogen sulfide to avoid being poisoned.

A number of other vent animals, including mussels (*Bathymodiolus*) and large clams (*Calyptogena*), contain symbiotic bacteria, though they can filter-feed as well. Non-symbiotic microbes are also an important food source. For example, the shrimp (*Rimicaris*) that dominates vent communities on the Mid-Atlantic Ridge scrapes off and eats bits of microbe-covered mineral from the chimneys that form at vents (see Fig. 2.26). The microbes are digested and the mineral eliminated.

Rimicaris do not have recognizable eyes, but they do have two light-sensitive patches on their upper surface. The patches can detect much fainter light than humans can see. Before the discovery that these shrimp could "see," no one suspected there was any light at all at deep-sea vents. A special low-light camera similar to those used to study distant stars revealed a faint glow, invisible to the human eye, around the vents. The source of the glow is uncertain, although some of it can be explained by the heat of the emerging water. Biologists speculate that the shrimp use this dim light both to locate active vents and to avoid getting cooked by coming too close to the scalding water.

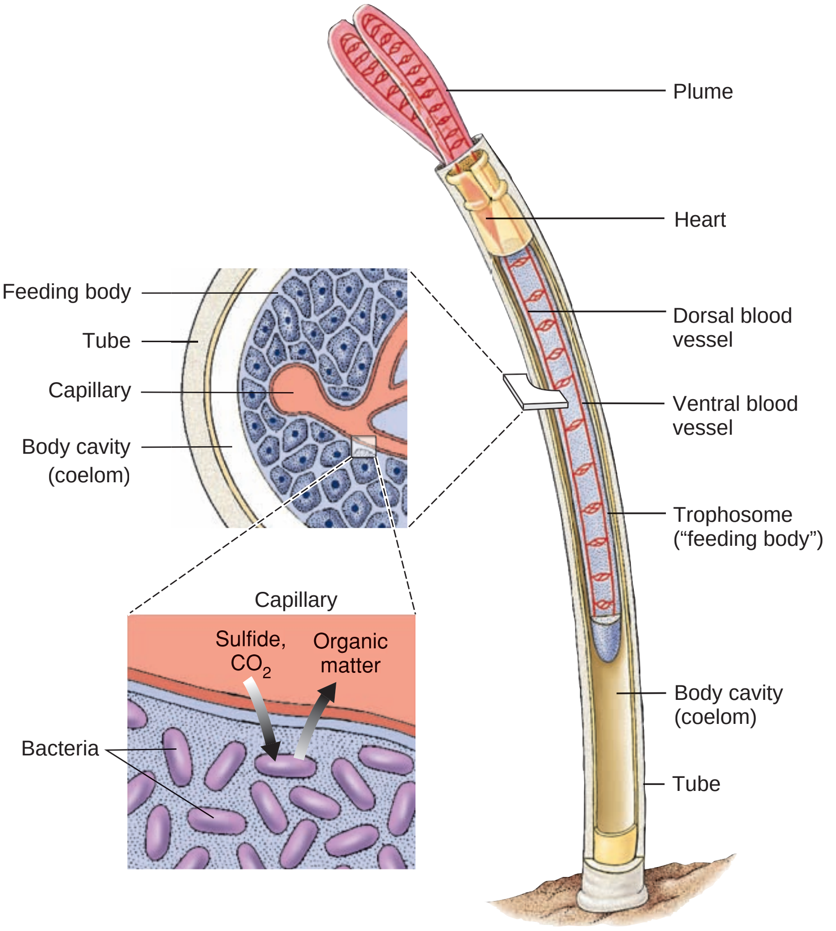


FIGURE 16.29 The anatomy of the giant hydrothermal-vent tubeworm (*Riftia pachyptila*). The plume at the end acts like a gill, except that it exchanges hydrogen sulfide (H_2S) as well as carbon dioxide (CO_2) and oxygen (O_2). The carbon dioxide and sulfide are carried in the blood to the feeding body, where symbiotic bacteria use them to make organic matter by chemosynthesis.

Boiling-hot black smokers are not the only hydrothermal habitat in the deep sea. "White smokers" occur a little further away from the active rift and are cooler, so that black sulphide minerals precipitate out before the water emerges from the sea floor. White minerals remaining in the water form the "smoke," "Snowblower vents" form when chemosynthetic bacteria living in rocks beneath the sea floor produce filaments of sulfur that coalesce into snowflake-like particles when they emerge from the vent into cold water. Cooler vents at greater distance from the mid-ocean ridge or associated with transform fault and trenches (see "The Mid-Ocean Ridge and Hydrothermal Vents," p. 37) support snails, sponges, deep-sea corals, and other organisms, but not in the abundance seen at mid-ocean ridge vents. Thick mats of chemosynthetic archaea and bacteria also grow in some of these areas, using carbonate minerals rather than sulfide minerals as an energy source. In 2007 Japanese researchers announced their discovery of "blue smokers": More expeditions are planned to investigate these.

Chemosynthetic communities aren't confined to hydrothermal areas. **Cold seeps** are places, mostly along continental margins or in sediment-rich basins like the Gulf of Mexico, where hydrogen sulfide and **methane** (CH_4) produced by the decay of organic matter seep out from the sea floor. Primary production by chemosynthetic prokaryotes that can use one or the other of these energy-rich molecules supports communities that are similar in many ways to those at hydrothermal vents, though the individual species are mostly different.

Communities based on chemosynthesis have even been found on deep-sea "graves." As previously discussed, occasional baitfalls like dead whales are an important source of food for deep-sea scavengers. When the scavengers are through, the decomposing remains produce hydrogen sulfide and methane, supporting a community similar to those at vents and seeps.

Unlike most deep-sea organisms, those at hot springs, cold seeps, and dead bodies enjoy an energy-rich environment and grow fast and large. On the other hand, their specialized habitats are tiny oases separated by vast distances. These oases are also unreliable. Hot springs and cold seeps can be wiped out by volcanic eruptions, undersea landslides, and other disturbances. As long as the flow of energy-rich molecules continues the communities recover fairly quickly, but sometimes the flow is blocked or dries up. In 2002 scientists returned to the Rose Garden, a hydrothermal vent near the Galápagos Islands first discovered in 1979 and revisited several times since, to find no trace of the rich vent community—only fresh lava flows. To avoid extinction, vent and seep species must be able to disperse to new oases, and indeed they do. Only 200 m (660 ft) from the Rose Garden site scientists discovered a new vent, dubbed "Rosebud," already colonized by juvenile tubeworms, clams, and mussels.

The carcasses of large organisms quickly rot away, so the species they support must also "island hop." The remains of whales, seals, sharks, and other large organisms are particularly tiny habitats in the expanse of the deep sea, but compared to hot springs and cold seeps there are a lot of them. Or at least there were. By hunting the giants of the sea to the brink of extinction, we may have already removed these stepping stones and doomed an entire ecosystem that we have only just discovered.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. The deep-sea floor has been considered as a potential site for the disposal of toxic and radioactive wastes. What questions about the biology, geology, and chemistry of the deep-sea environment do you think should be answered before such plans are approved?
2. How do you think non-migratory midwater fishes, with their flabby muscles, are able to prey on vertical migrators, which have well-developed muscles?
3. Fats are highly energy-rich molecules that require a great deal of energy to produce, but in the mesopelagic, where food is scarce, many fishes have swim bladders filled with fat. How might this be explained?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Dybas, C. L., 1999. Undertakers of the deep. *Natural History,* vol. 108, no. 9, November 1999, pp. 40–47. Whale carcasses on the sea floor support islands of diverse, recently discovered marine life. Check out this article's web page for video.

Dybas, C. L., 2004. Close encounters of the deep-sea kind. *BioScience,* vol. 54, no. 10, October, pp. 888–891. Deep-sea exploration from submersibles.

Fildes, J., 2005. Dive dive dive. *New Scientist,* vol. 187, no. 2517, 17 September, pp. 26–30. Scientists are gearing up for a new wave of deep-sea exploration.

Kunzig, R., 2001. The physics of deep-sea animals. They love the pressure. *Discover,* vol. 22, no. 12, December, pp. 40–47. A look at how the inhabitants of the deep sea cope with the enormous pressure.

Levin, L. A., 2002. Deep-ocean life where oxygen is scarce. *American Scientist,* vol. 90, no. 5, pp. 436–444. The distribution and causes of oxygen minimum zones, and the adaptations of the organisms that live in them.

Lutz, R. A., 2003. Dawn in the deep. *National Geographic,* vol. 203, no. 2, February, pp. 92–103. A scientific film project lights up the world of hydrothermal vent communities.

Lutz, R. A., T. M. Shank, and R. Evans, 2001. Life after death in the deep sea. *American Scientist,* vol. 89, no. 5, September/October, pp. 422–431. A hydrothermal vent community recovers after a volcanic eruption.

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Nicholls, H., 2004. Sink or swim. *Nature,* vol. 432, no. 7013, 4 November, pp. 12–14. Biodiversity on seamounts and in other open-ocean habitats is in trouble.

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The deep, 2005. *New Scientist,* vol. 188, no. 2525, 12 November, pp. 36–51. A 15-page special with spectacular photos and articles about new deep-sea discoveries.

In Depth

Koslow, J. A., 1997. Seamounts and the ecology of deep-sea fisheries. *American Scientist,* vol. 85, no. 2, March/April, pp. 168–176.

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Levin, L. A., R. J. Etter, M. A. Rex, A. J. Gooday, C. R. Smith, J. Pineda, C. T. Stuart, R. R. Hessler, and D. Pawson, 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics,* vol. 32, pp. 51–93.

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Sokolova, M. N., 1997. Trophic structure of the abyssal benthos. *Advances in Marine Biology,* vol. 32, pp. 427–525.

Warrant, E. J. and N. A. Locket, 2004. Vision in the deep sea. *Biological Reviews,* vol. 79, pp. 671–712.

Part Four

Humans and the Sea

17

CHAPTER

Resources from the Sea

Catch of the day, Chile.

People have used the many resources that the oceans offer ever since the first humans ventured to the shore. Evidence of the use of marine life as food goes back to prehistoric times and includes fishhooks, seashell artifacts, and mounds of empty mollusc shells. Our exploitation of marine resources is now much more sophisticated (Fig. 17.1), but, unfortunately, it has also become more destructive. Fishers cross the oceans assisted by satellites, marine chemists extract wonder drugs from marine organisms, genetic engineers develop faster-growing fish, and ocean engineers investigate better ways of harvesting energy from waves and tides.

Chapter 17 examines the resources of the sea and their use, and misuse, by humans. In discussing them we will draw on our knowledge of the sea floor and the chemical and physical features of the ocean (discussed in Part One of the book) and of the types and distribution of marine life (discussed in Parts Two and Three). Many other disciplines, ranging from technology development to the marketing of new products, are also involved.

THE LIVING RESOURCES OF THE SEA

The oceans, which cover most of the surface of the earth, are the planet's largest factory of organic matter. Humans take advantage of this productivity and harvest many different kinds of marine organisms. Most are harvested for food, but they also provide many other products and materials. Millions of people also use the living resources of the sea in recreational fishing, sport diving, or even by keeping an aquarium at home.

Food from the Sea

The oceans provide food as well as employment for millions of people. Many different types of marine organisms are harvested. Seaweeds and creatures as diverse as jellyfishes, sea cucumbers, and even polychaete worms are part of the diet in many cultures. The vast majority of the harvest, however, consists of fishes, which are known in fisheries terminology as **finfish.** Finfish constitute nearly 90% of the total world marine catch. Molluscs and crustaceans, which together are called **shellfish,** are less important than finfish in the size of their catch but the value of the catch is very significant.

Most of the world's food is grown on land, and food from the sea represents only about 1% of all the food eaten. Still, seafood is one of the world's most important foods. It is rich in protein, which is essential for normal growth. Finfish, ocean catches and aquaculture figures combined, provides around 30.4% of the animal protein consumed by people around the world. Dependence on seafood for protein is much higher in most coastal nations, especially poor ones. The world's population is still growing (Fig. 17.2), and it is increasing much faster in the places where it hurts the most: the poor, already crowded countries of the developing world.

The groups of marine organisms that are most widely used as food are fishes, molluscs, and crustaceans. Seafood is important to the world's population because it is a good source of protein.

Marine fisheries provide much-needed employment and profit. As we shall see, however, the world's most important fisheries are already overexploited, and some are exhausted. Worldwide catches had stabilized despite increasing effort by the late 1980s (Table 17.1) after increasing almost fivefold since 1950. Neither the world fish catch nor the world grain output may be able to catch up with global population growth. The amount of grain and fish per person has already started to decrease. The Food and Agriculture Organization (FAO) of the United Nations has estimated that by 2010 world demand for fish will be 10 to 40 million tons above production. The world's oceans have been running out of fish mostly because of overfishing.

FIGURE 17.1 Northern bluefin tuna (*Thunnus thynnus*) being unloaded from a freezer ship to a modern cannery. The valuable catch is canned for human consumption and the by-products processed into pet food, fertilizer, and chicken feed for sale around the world.

Fishing is one of the oldest human endeavors. Small-scale fisheries that involve simple gear and methods are still practiced around the world, especially in developing countries. These fisheries, in fact, employ most of the world's fishing people. They also provide animal protein to people whose diets are often protein-deficient.

The increased demand for seafood in affluent countries and the expansion of the world's population have steadily increased the pressure on the food resources of the sea (Fig. 17.3). The application of technology, from the development of more effective gear to the use of satellites to find fish, has greatly increased the efficiency with which we harvest these resources. Nations like China, Japan, South Korea, and the United States have developed high-tech fishing fleets that can remain on the fishing grounds away from the home port for long periods. Factory, or mother, ships process and store the fish taken by smaller fishing boats. The catch is processed, marketed,

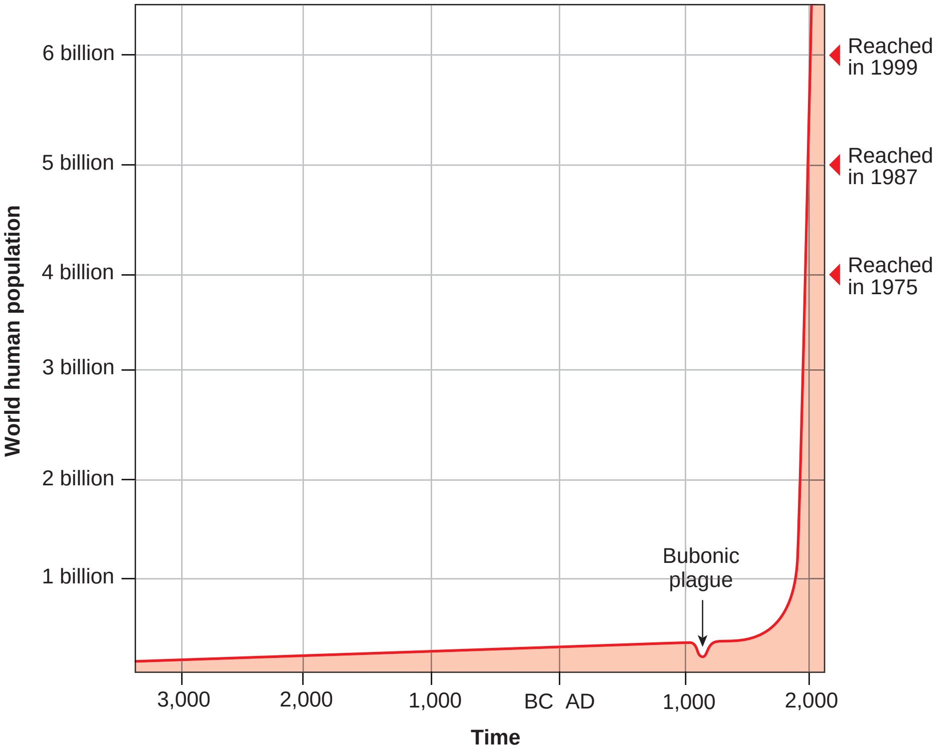


FIGURE 17.2 The curve that represents the growth of the world human population over the centuries looks like a giant J: Very slow, almost non-existent population growth is followed by a sudden explosion of very fast growth. This J-shaped curve indicates that the more people there are, the faster the population grows, as was the case with the dinoflagellates shown in Figure 10.2. Growth was slow for millennia because of food shortages and disease. The domestication of plants and animals helped provide more food, but periodic famines and plagues, like the bubonic plague in Europe during the 1300s, kept the population in check. Better sanitation, advances in medicine, and more efficient agriculture eventually helped sharply reduce the death rate, and within a few centuries the population began to increase rapidly. A decrease in the birth rate of many countries, however, has slowed down global population growth. In addition, AIDS has significantly increased mortality in many countries. In 2005 the United Nations projected a world population of 9.1 billion by 2050. The population of the United States continues to grow, reaching 300 million in 2006.

Table 17.1 **World Commercial Catches of Selected Fishes, Molluscs, and Crustaceans in Millions of Metric Tons**

Catch	1975	1980	1985	1990	1995	2000	2004
Herrings, sardines, etc.	13.43	16.14	21.10	22.32	22.01	24.90	23.26
Miscellaneous pelagic fishes	not listed	not listed	not listed	not listed	13.93	10.64	11.17
Cods, haddocks, hakes, pollocks	11.85	10.75	12.46	11.58	10.74	8.68	9.43
Tunas, bonitos, billfishes	2.06	2.55	3.18	4.43	4.89	5.82	6.02
Salmon, smelts	0.55	0.80	1.17	1.51	1.15	0.80	0.88
Flounders and other flatfishes	1.16	1.08	1.35	1.23	0.92	1.01	0.87
Sharks, rays	0.59	0.60	0.62	0.69	0.76	0.87	0.81
Total marine fishes	**51.93**	**55.73**	**64.40**	**69.36**	**72.00**	**71.84**	**71.55**
Freshwater fishes	5.96	6.17	8.74	12.23	5.80	6.80	7.85
Squids, octopuses	1.18	1.53	1.79	2.36	2.94	3.66	3.77
Clams, cockles	0.94	1.20	1.51	1.53	0.96	0.80	0.85
Scallops	0.29	0.37	0.60	0.87	0.54	0.66	0.80
Mussels	0.53	0.62	0.97	1.34	0.24	0.26	0.19
Oysters	0.85	0.97	1.09	1.00	0.19	0.25	0.15
Total marine molluscs	**4.03**	**4.91**	**6.18**	**7.73**	**6.38**	**7.25**	**6.89**
Shrimps	1.33	1.70	2.12	2.63	2.44	3.08	3.60
Crabs	0.75	0.82	0.89	0.89	0.95	1.09	1.36
Lobsters	0.10	0.10	0.20	0.21	0.22	0.23	0.23
Krill	0.04	0.48	0.19	0.37	0.12	0.11	0.12
Total marine crustaceans	**2.35**	**3.20**	**3.42**	**4.50**	**4.77**	**5.91**	**5.70**
World total catch in marine fishing areas	**61.22**	**64.46**	**75.68**	**82.25**	**85.04**	**86.80**	**85.79**

Note: Catches tabulated in groups defined by the Food and Agriculture Organization of the United Nations; only selected groups are listed and, when added, will not equal totals.

and sold in a multitude of ways: fresh, frozen, canned, dried and salted, smoked, marinated, as fish sticks, and as fish meal. Fishing operations have been known to diversify into businesses that develop new products such as boats and fishing gear. Some even get involved in the management of fishing resources to prevent them from disappearing. Modern fishing ventures thus provide jobs not only to fishers but also to technicians, marine biologists, marketing specialists, economists, and other experts. Women and the elderly often undertake processing and marketing in developing countries, which contributes to social equity. Commercial fisheries provide a considerable portion of the export earnings of countries like Canada and Iceland and help sustain these nations' economies.

The amount of seafood consumed in various cultures varies widely because of consumer tastes, price, and availability. The average Japanese eats 17.1 kg (37.7 lb) of fish a year, while Americans consume an average of 7.5 kg (16.6 lb) per person a year. Seafood consumption has been steadily increasing in the United States, Canada, and other developed countries as consumers broaden their tastes and look for healthy, low-fat sources of protein.

Major Fishing Areas Most of the world's major fisheries are located near the coast (Fig. 17.4). These coastal fisheries exploit the rich waters of the **continental shelf.** Because shelf waters are shallow compared with the open ocean, it is relatively easy to harvest bottom-dwelling, or **demersal,** species. Coastal fisheries also include **pelagic** catches: fishes, squids, and other animals that live in the water column. **Primary production** is higher over the shelf than farther offshore, supporting much more abundant life (see Table 10.1, p. 225, and Fig. 15.26). Significant coastal fisheries are found where the continental shelf is very wide, such as the Grand Banks of Newfoundland, the North Sea, and the Bering Sea.

Most of the world's fisheries are coastal. Coastal fisheries take both bottom, or demersal, and open-water, or pelagic, catches. Other valuable fisheries are found in the open ocean far from the coast.

Continental Shelf The shallow, gently sloping edge of the continents, extending from the shore to the *shelf break,* the point where the slope gets steeper.

- Chapter 2, p. 33; Figure 2.19

Primary Production The conversion by autotrophs of carbon dioxide into organic carbon, that is, the production of food.

- Chapter 4, p. 68

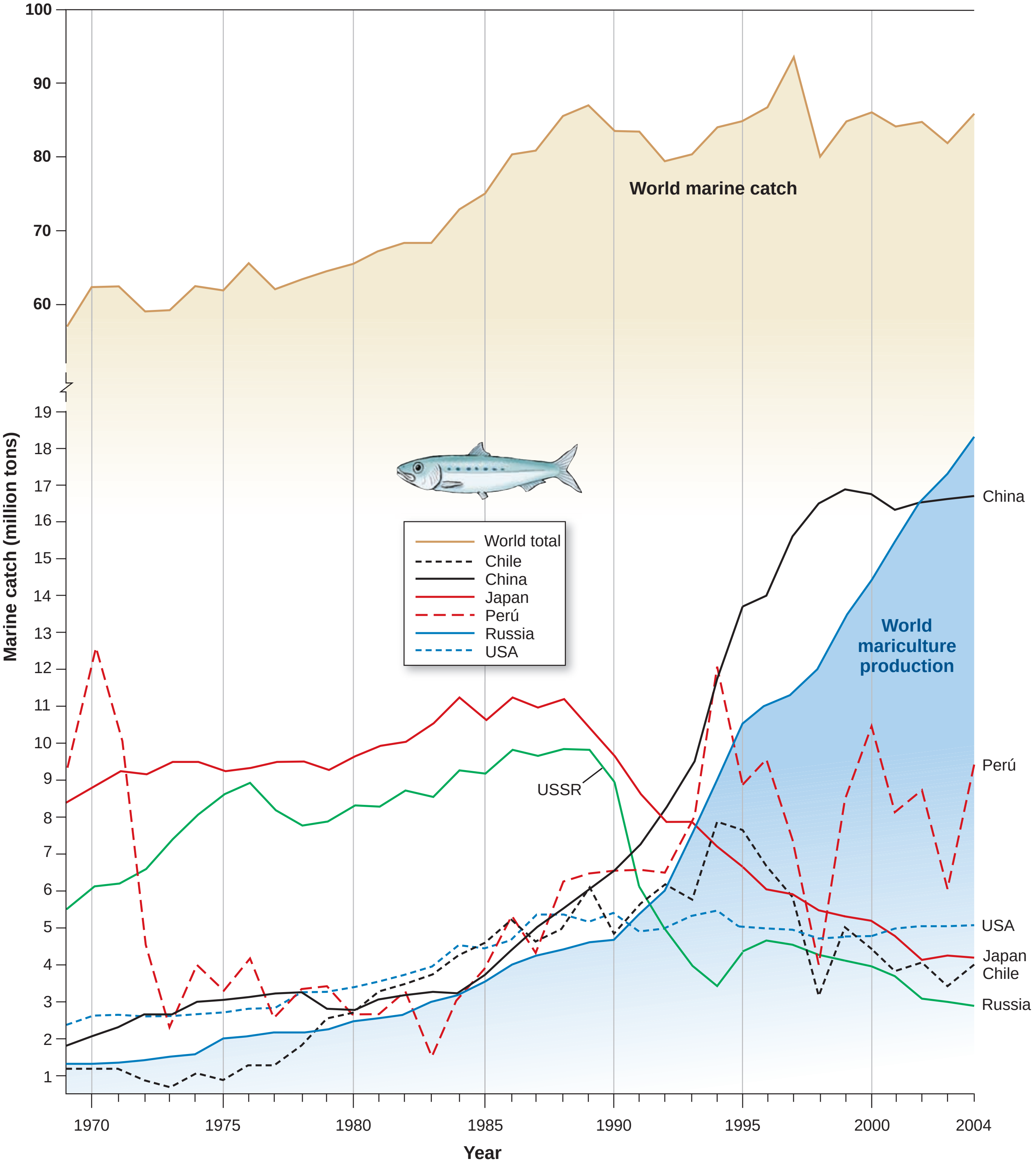


FIGURE 17.3 World marine catch, world mariculture production, and catches by the world's six major fishing nations. Marine fishes constitute the bulk of the catches, but shellfish are also included. Notice that annual catches by two of the leading nations, Japan and Russia, have decreased since the late 1980s. Economic and political instability have affected Russian catches, which until 1990 included those from the former Soviet Union. The figures for Perú (and Chile to some extent) show the dramatic ups and downs of its huge anchovy fishery (see "Of Fish and Seabirds, Fishers and Chickens," p. 389). Chinese catch statistics may be inflated by a tendency of local managers to overstate catches to enhance their promotion prospects. Thus, global catches may have actually declined instead of remaining more or less stable as shown here.

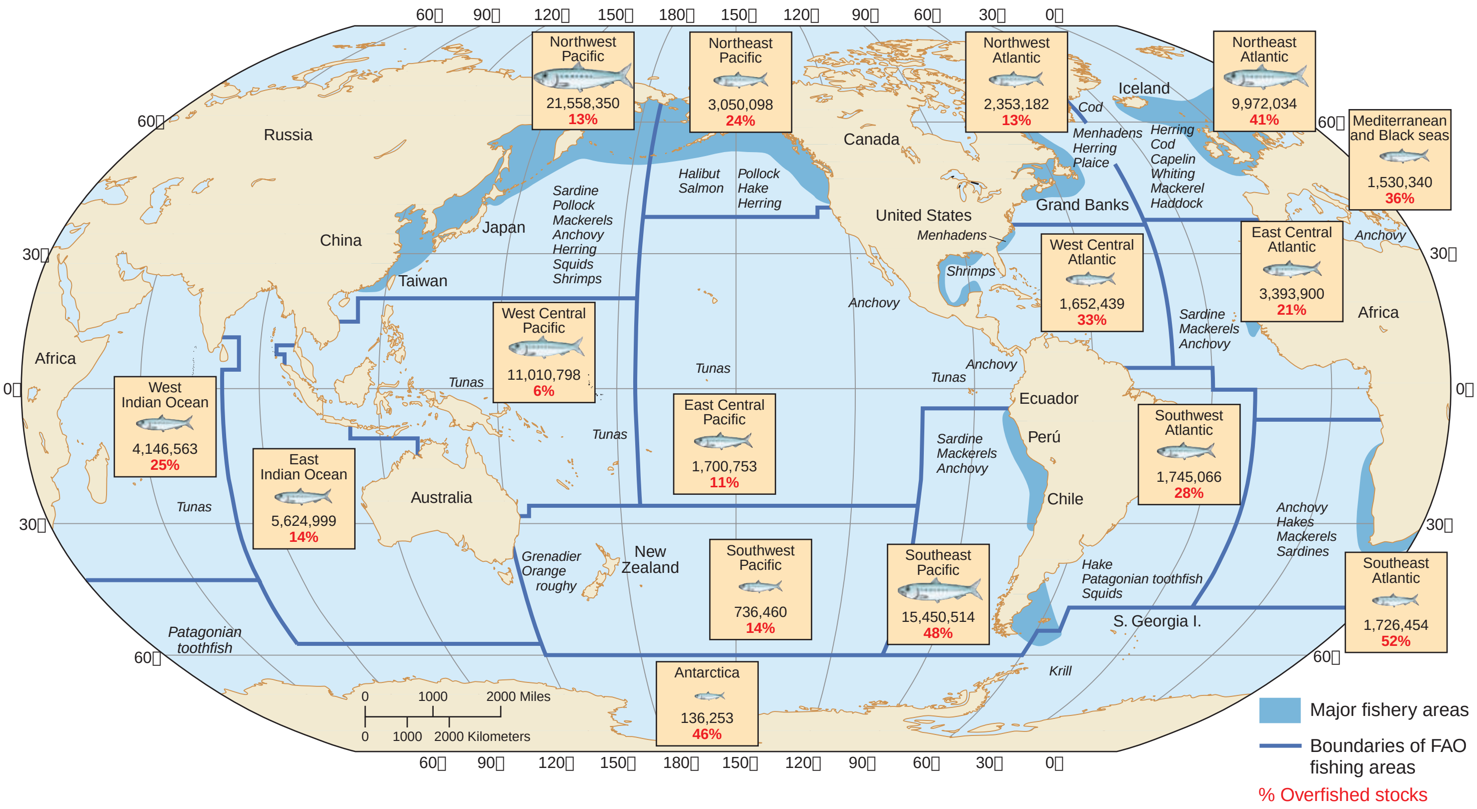

60° 90° 120° 150° 180° 150° 120° 90° 60° 30° 0°
Northwest Pacific
21,558,350
13%
Northeast Pacific
3,050,098
24%
Northwest Atlantic
2,353,182
13%
Northeast Atlantic
9,972,034
41%
Mediterranean and Black seas
1,530,340
36%
Russia
China
Japan
Taiwan
Canada
Iceland
United States
Africa
Sardine
Pollock
Mackerels
Anchovy
Herring
Squids
Shrimps
Halibut
Salmon
Pollock
Hake
Herring
Cod
Menhadens
Herring
Plaice
Herring
Cod
Capelin
Whiting
Mackerel
Haddock
Grand Banks
Menhadens
Shrimps
Anchovy
West Central Atlantic
1,652,439
33%
East Central Atlantic
3,393,900
21%
Anchovy
Sardine
Mackerels
Anchovy
West Central Pacific
11,010,798
6%
Tunas
Tunas
Anchovy
Tunas
Ecuador
Perú
Chile
West Indian Ocean
4,146,563
25%
East Indian Ocean
5,624,999
14%
East Central Pacific
1,700,753
11%
Tunas
Sardine
Mackerels
Anchovy
Southwest Atlantic
1,745,066
28%
Australia
Tunas
Anchovy
Hakes
Mackerels
Sardines
Grenadier
Orange roughy
New Zealand
Southwest Pacific
736,460
14%
Southeast Pacific
15,450,514
48%
Hake
Patagonian toothfish
Squids
S. Georgia I.
Southeast Atlantic
1,726,454
52%
Patagonian toothfish
Krill
Antarctica
136,253
46%
0 1000 2000 Miles
0 1000 2000 Kilometers
60° 30° 0° 30° 60°
Major fishery areas
Boundaries of FAO fishing areas
% Overfished stocks

FIGURE 17.4 The major marine fishing areas of the world, based on boundaries established by the Food and Agriculture Organization of the United Nations (FAO). Figures refer to the 2004 marine fish and shellfish catches (in millions of tons) of each region. Figures in red refer to the percent (%) overfished stocks. The figure for Antarctica incorporates catches for three separate FAO regions. Half of the 18 FAO regions showed higher catches in 2004 than in 2003. These figures do not include illegal fishing, particularly for Patagonian toothfish in Antarctic and subantarctic waters.

Notice from the map in Figure 17.4 that some of the largest catches are taken from the northwest Pacific and the northeast Atlantic. Being close to the major industrial nations, these areas have been intensively exploited for the longest time. Most fishing grounds in the Atlantic, Pacific, and Mediterranean are in decline or exhausted. A few other areas are less heavily exploited and still have some underexploited resources. This is the case in the Indian Ocean and around Antarctica. These areas are more remote and therefore more expensive to exploit. Fisheries in such remote areas, however, are rapidly increasing.

The open ocean, 92% of the total area of the ocean, supports fewer fisheries than the continental shelf but they are nevertheless very valuable. Some of the richest fishing areas of the world are located in **upwelling** areas just beyond the continental shelf, including those of Perú and northwest Africa (Fig. 17.4). Other fisheries, like those for migratory species like tunas, extend far into the open ocean.

Major Food Species There are thousands of species of fishes, crustaceans, and molluscs, but relatively few support major fisheries. A summary of the major commercial catches for the world is given in Table 17.1.

The largest catches in the world are those for **clupeoid fishes,** small, **plankton-feeding** fishes that form huge schools. They include herrings (often sold as "sardines"), anchovies, sardines (sometimes called pilchards), menhadens, and shads (Table 17.2). Clupeoid fishes are usually concentrated over the continental shelf, but some species can also be found offshore in upwelling areas. They are caught with large **purse seines** that surround and trap the schools (Figs. 17.5*b* and 17.6*b*).

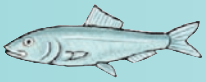
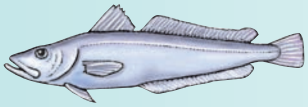
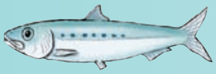
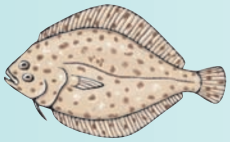
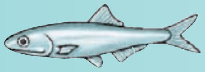
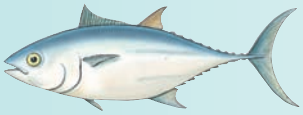
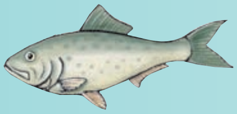
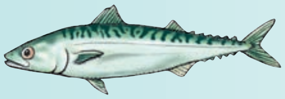
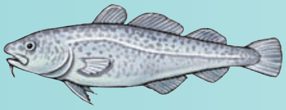
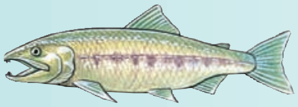
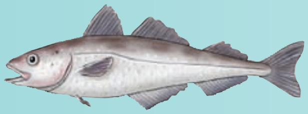
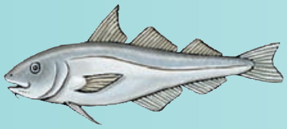
Herrings, anchovies, and sardines are eaten fresh, canned, or pickled. **Fish protein concentrate (FPC),** or **fish flour,** an odorless powder used as a protein supplement for human consumption, is also made from these and other fishes. Most of the clupeoid catch, however—particularly that of menhadens and herrings—is ground into **fish meal,** an inexpensive protein supplement used in feed for poultry, livestock, and even other species of fish that are farmed. The fish are also pressed to obtain **fish oil,** used in the manufacture of products like margarine, cosmetics, and paints. Some of the catch finds its way into fertilizers and pet food. Fisheries such as these, where the catch is used for purposes other than direct human consumption, are now estimated to account for over a third of the world's total.

Clupeoid fishes, herrings and their kin, provide the largest catches of fish. Most are used not directly as food but in fish meal and other products.

Upwelling The upward flow of nutrient-rich deep water to the surface, resulting in greatly increased primary production.
- Chapter 15, p. 351

Plankton-feeding fishes use gill rakers, slender projections of the gills, to strain plankton from the water.
- Chapter 8, p. 161

Table 17.2 Examples of Commercially Important Fishes around the World

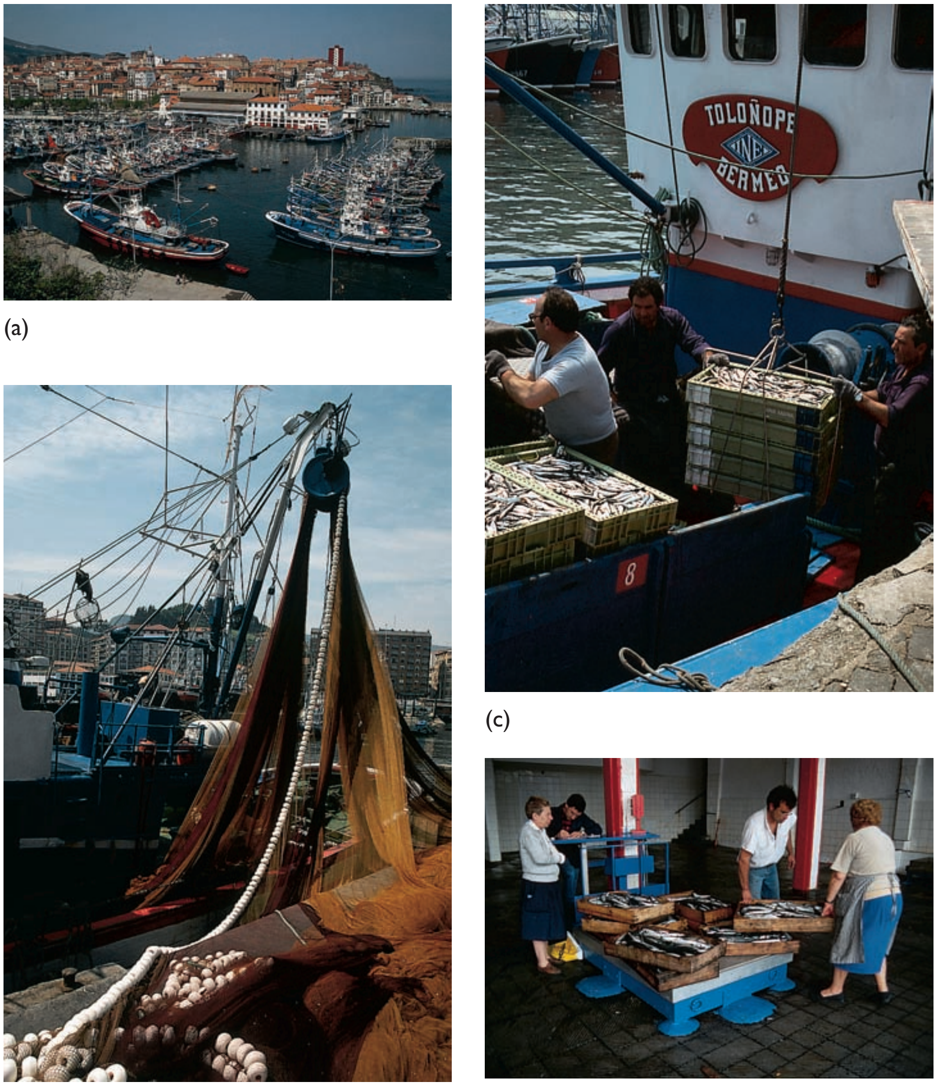
Species	Distribution and Habits	Species	Distribution and Habits
 Herrings (*Clupea*)	North Atlantic and Pacific; schooling, plankton feeders; 38 cm (15 in)	 Hakes and whiting (*Merluccius*)	Temperate worldwide; demersal, feed on bottom invertebrates and fishes; 1 m (3 ft)
 Sardines, or pilchards (*Sardinops, Sardinella, Sardina*)	Mostly temperate worldwide; schooling, plankton feeders; 30 cm (12 in)	 Flatfishes: flounders, halibuts, soles, and others (*Platichthys, Hippoglossus*, etc.)	Mostly temperate worldwide; demersal, feed on bottom invertebrates and fishes; 2 m (6.5 ft) in some halibuts
 Anchovies (*Engraulis*)	Worldwide; schooling, plankton feeders; 20 cm (8 in)	 Tunas (*Thunnus, Katsuwonus*, etc.)	Tropical and temperate; schooling, carnivores; 4.3 m (14 ft) in the bluefin tuna
 Menhadens (*Brevoortia*)	Temperate and subtropical Atlantic; schooling, plankton feeders; 38 cm (15 in)	 Mackerels (*Scomber, Scomberomorus*)	Tropical and temperate worldwide; schooling, carnivores; 2.4 m (8 ft)
 Cods (*Gadus*)	North Atlantic and Pacific; demersal, feed on bottom invertebrates and fishes; 1.5 m (5 ft) in the Atlantic cod (no longer this large)	 Salmon (*Oncorhynchus, Salmo*)	North Pacific and Atlantic; open ocean and rivers, carnivores; 1 m (3 ft)
 Alaska, or walleye, pollock (*Theragra chalcogramma*)	Temperate North and Central Pacific; demersal, feeds mostly on bottom invertebrates and fishes; 90 cm (35 in)		
 Haddock (*Melanogrammus aeglefinus*)	North Atlantic; demersal, feeds mostly on bottom invertebrates; 90 cm (35 in)		

Note: Fishes are not drawn to scale. The measurements given are the approximate maximum length.

Cods and related fishes—the pollock, haddock, hakes, and whiting (Table 17.2)—make up another important component of the worldwide catch. These fishes are all demersal, cold-water species. They are mostly caught with **trawls** that are dragged along the bottom (Fig. 17.6*d*). The Alaska, or walleye, pollock (*Theragra chalcogramma*) is the largest fishery in U.S. waters.

The Atlantic cod (*Gadus morhua*) supported a very important fishery for centuries. European fishers were already fishing for it on the Grand Banks of Newfoundland a century before the arrival of the first colonists (and probably before Columbus). It was a vital source of inexpensive protein in many parts of the world. In an age before refrigeration, cod was salted and dried for preservation before being sent to Europe and the Caribbean. The dried fish was soaked in water before cooking, just as it is done today in the Mediterranean and Caribbean. Now, however, most cods and related fishes are sold fresh or frozen.

The cod fishery on the Grand Banks lasted until 1992 when a moratorium was declared in an attempt to save the fishery from extinction. The fishery had peaked in the late 1960s, almost 25 years before the moratorium. The Georges Bank fishery off New England was similarly closed in 1994, that off Newfoundland and Labrador in 2003. The closures caused high unemployment among Canadian and American fishers and related workers, as well as higher prices for consumers. The closures also threaten to destroy traditional fishing cultures. But even worse, some



(a)

(b)

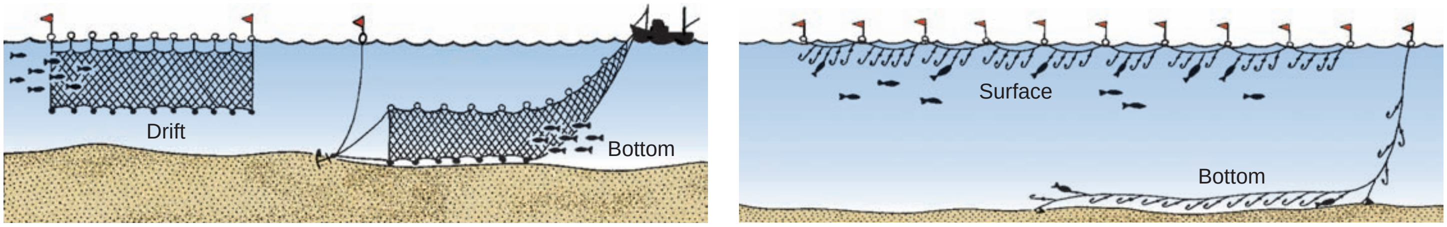
(c)

(d)

FIGURE 17.5 The European anchovy (*Engraulis encrasicholus*) is an important food fish. It is canned, salted, or cooked fresh. Basque fishers from the port of Bermeo (*a*) in the Bay of Biscay, northern Spain, make bountiful catches using purse seines (*b*). Fish is unloaded (*c*) and sold in the fish market (*d*). Women workers, or *neskatillas,* play an important role in the fishing routine. They are in charge of carrying and selling the fish.

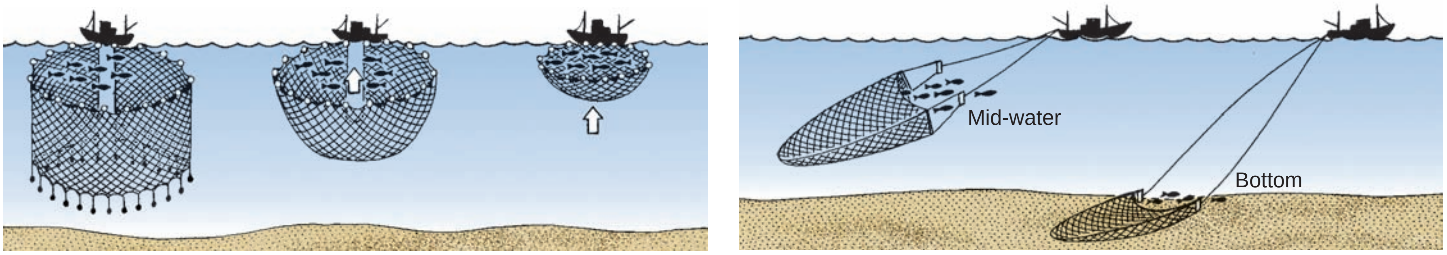
experts predict that the cod populations will never recover. It appears that juvenile cod have little chance of surviving because fishes such as herring and mackerel, which are normally eaten by adult cod, are now feeding on the juveniles. Cod is now listed as an endangered species in Newfoundland, unthinkable a few decades ago. Cod fisheries are also exhausted elsewhere in the North Atlantic. North Sea catches dropped from 277,000 metric tons in 1971 to 59,000 metric tons in 2000. As a result, vast areas were closed to cod fishing in 2001. Cod, however, is now commercially farmed in Norway (see Table 17.3).

Jacks, mullets, rockfishes (including the ocean perches, also known as redfishes), and mackerels (Table 17.2) are also important in terms of worldwide tonnage. Canned mackerel from Japan, South America, and elsewhere has become an important source of cheap protein in some parts of the world. Flounders, halibuts, and other flatfishes are important catches in the United States, Canada, and other countries. Salmon, though now caught in much smaller numbers than formerly, are a very valuable catch. The salmon fishery is still important in the North Pacific in terms of the



(a) Gill nets

(c) Longline



(b) Purse seine

(d) Trawls

FIGURE 17.6 Examples of fishing methods.

FIGURE 17.7 Octopuses have long been valued as a culinary delicacy. These freshly caught individuals were cleaned and left to dry on the Greek island of Paros in the Aegean Sea.

FIGURE 17.8 Raw fish, shrimp, seaweed, scallops, and sea urchin roe are used in *sushi* and *sashimi,* Japanese delicacies that have become popular around the world.

dollar value of the catch. Salmon are caught both along the coast and in the open ocean. The fishery is threatened, however, by overfishing and environmental degradation, especially the destruction of salmon breeding sites (see "Migrations," p. 168). Most of the salmon consumed now is farmed.

The most important open-ocean fisheries are those for several species of tunas (Table 17.2). The migration routes of tunas crisscross the oceans, mostly in tropical waters (see Fig. 8.22). Skipjack, yellowfin, albacore, bigeye, and bluefin tunas command high prices in world markets. Most are eaten in affluent countries, either canned or raw as *sashimi.* They are caught by modern fleets that use sophisticated techniques to spot the schools in mid-ocean. The fishes are caught with large seines, surface **longlines,** or **gill nets** (Fig. 17.6). The fishing boats are equipped with freezers so that the fishes can be brought to port long after they are caught. Besides these high-tech fleets, some local, small-scale fisheries continue to exploit bonito, skipjack, and other tunas.

Molluscs are the second most valuable group of marine food species after fishes. Several types of **cephalopods** provide the largest catches of molluscs (Table 17.1). Squids, cuttlefishes, and octopuses are especially popular in Far Eastern and Mediterranean countries (Fig. 17.7). Fishers use lighted boats to catch squid at night. Other important food molluscs are clams (*Macoma* and many others), oysters (*Ostrea*), mussels (*Mytilus*), scallops (*Pecten*), and abalones (*Haliotis*).

Crustaceans are prized as food the world over. Major fisheries exploit many species of shrimps and lobsters, all of which bring a high price. Crabs such as the blue (*Callinectes sapidus*), king (*Paralithodes camtschaticus*), and Dungeness (*Cancer magister*) are also harvested. *Langostino* (some species of *Cervimunida* and *Pleuroncodes*), sometimes called "langostino lobster" or "squat lobster," has become an important food item. It is neither a true lobster nor a shrimp but a galatheid crab more related to hermit crabs (see Fig. 17.13 for a similar species of *Pleuroncodes*).

Other groups of marine organisms are also eaten (Fig. 17.8), though they do not contribute much to global fisheries production. Seaweeds, for instance, are eaten in many cultures, especially in the Far East (see "Seaweeds for Gourmets," p. 111). Sea urchins are esteemed for their gonads, or roe, which command an astronomical price, particularly in Japan. In California there is a fishery for the red sea urchin (*Strongylocentrotus franciscanus*). Most of the roe is exported to Japan or sold to Japanese restaurants where, known as *uni,* it is eaten raw. Some species of sea cucumber are another common seafood. Called *trepang* or *bêche-de-mer,* they are dried, boiled, smoked, or eaten raw in the Orient. Examples of other invertebrates used as food are jellyfishes in the Orient, gooseneck barnacles in Spain, and polychaete worms in the South Pacific.

Sea turtles are still hunted and their eggs still gathered, even where they are officially protected. Seals and whales are also eaten in some places, and there are traditional fisheries for marine mammals in the Arctic (see Fig. 4.2), North Atlantic, West Indies, and South Pacific. These traditional fisheries are a source of considerable controversy because most of the species involved are endangered and modern technologies like powerboats are used. Should traditional fisheries be banned or left entirely unregulated? A compromise between these two extremes involves questions of the rights of indigenous cultures, the ethics of conservation, and international politics.

Optimal Yields and Overfishing Like all living things, species we harvest for food can reproduce to replace the individuals that are lost to disease and predators, including humans. Because these living resources can replace themselves, they are known as **renewable resources.** Resources that are not naturally replaced, like oil and minerals, are called **non-renewable resources** (see "Non-Living Resources from the Sea Floor," p. 396). Experience has shown, however, that, though the food resources of the ocean are renewable, they are not inexhaustible.

Imagine that fishers discover a new, untapped population of sardines. The new fishery is very successful, and the fishers make handsome profits. The news spreads, and soon other fishers join in. After several years, **overfishing** results: Catches dwindle, and the fish caught are smaller. The fishery becomes unprofitable, and many, if not most, of the fishers go out of business.

What happened? The reproductive rate of sardines—or salmon, scallops, or sharpnose surfperches—depends, at least in part, on the size of the population, or **stock,** as it is known to fisheries biologists. Like dinoflagellates growing in a jar (see Fig. 10.2), fish stocks grow fastest when there are neither too few nor too many individuals in the population. If the population size is very small, the number of young being born is also small because there are not many potential parents. If the population is too large, competition, overcrowding, and diseases slow down the growth rate. The number of new young, that is, the population growth rate, is highest at some intermediate population density (Fig. 17.9).

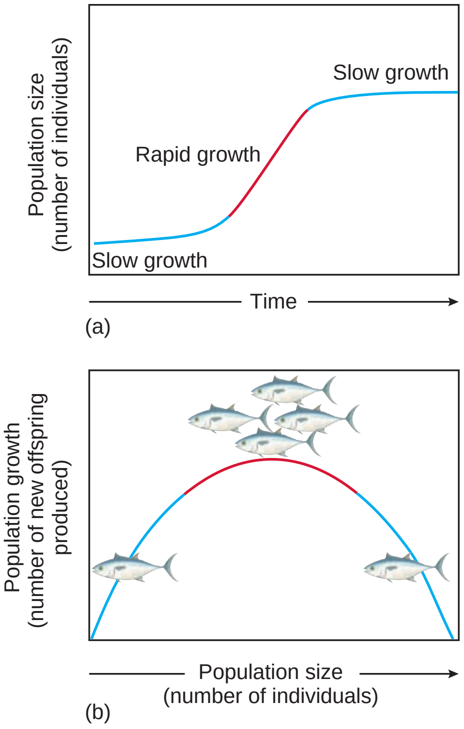


FIGURE 17.9 (*a*) The theoretical growth of a population that begins with just a few individuals. At first, with only a few adults to produce offspring, the population increases very slowly (blue line). As the population size gradually increases, so does the number of offspring, and the rate of growth begins to increase (red line). Eventually, the population reaches the point where limiting factors such as food shortage and crowding prevent further growth (blue line). (*b*) Thus, the rate of growth is directly related to population size and is maximal at intermediate abundances. Also see Figure 10.4.

To harvest the stock in the optimal way, one must consider this feature of population growth. Obviously, it would be foolish to harvest the entire stock at once, because no individuals would be left to reproduce, and the fishery would be destroyed forever. If the fishery is to last indefinitely, or to be **sustainable,** the number of fish caught can be no more than the number of new fish added through reproduction; if more are caught, the population will decline. The **sustainable yield** of a population is the amount that can be caught and just maintain a constant population size. In other words, the catch is just large enough to prevent the population from growing but not so large as to reduce it.

Because the growth rate depends on the population size, so does the sustainable yield. When the stock is large, it is held in check by natural mortality; even a small harvest causes a reduction in the population. Very small populations also have a low growth rate. In this case, fishing is more dangerous because it can threaten the seed stock and drive the species to the brink of extinction.

The highest catch that can be continued year after year without threatening the stock is called the **maximum sustainable yield.** It occurs at medium population size, when the natural growth rate is highest. From the point of view of profit and food production, this can be thought of as the optimal catch.

The size of the catch, and therefore of the stock, is directly related to **fishing effort:** how many boats and fishers there are, how long they stay at sea, and so forth. When little effort is put into the fishery, of course, the catch is small. Only a small fraction of the stock is removed by fishing, and the population grows until limited by natural factors. The population remains secure, but the fishery yields less food and less profit than it could safely sustain.

With intense effort the catch exceeds the maximum sustainable yield. Before long the stock declines and catches fall no matter how much fishing effort is expended: Overfishing has occurred.

A plot of the sustainable yield versus fishing effort gives us a **catch-effort curve,** which is very similar to a plot of the population growth rate versus the size of the stock (Fig. 17.10). The maximum sustainable yield occurs at moderate levels of effort, which result in intermediate stock sizes.

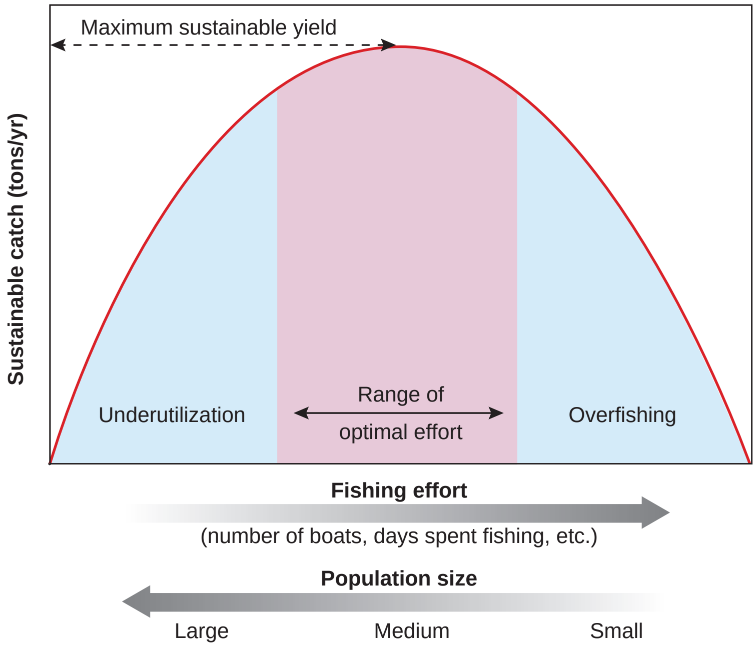


FIGURE 17.10 A generalized, theoretical curve showing that, as fishing effort increases, so does the catch, but only up to a point, which is the biologically optimal catch. After this point the overexploited fishery will yield smaller and smaller catches as the effort increases. The curve is called a catch-effort curve.

Unfortunately, the biological properties of most fisheries stocks do not mix well with the principles of economics. Most fisheries are profitable when harvested at the level of the optimum catch. As long as there is money to be made, more fishers and more boats will be attracted to the fishery, and the catch will exceed the optimal level. In an open fishery, one that

Cephalopods Squids, octopuses, and related molluscs that use sucker-bearing arms to capture prey and, with a few exceptions, lack a shell.
- Chapter 7, p. 130

is completely unregulated, market forces inevitably lead to overfishing. A fishery may still be profitable to some fishers, even if below the maximum sustainable yield. The total profit from the fishery, however, decreases.

Overfishing results when catches are higher than the maximum sustainable yield, or optimal catch, of a fishery. Free-market forces almost always result in overfishing if a profitable fishery is left unregulated.

Overfishing is not just a theoretical problem. FAO has estimated that over 70% of all marine commercial fisheries are fully exploited or depleted. Good examples are the stocks of cod, herring, halibut, salmon, Alaskan king crab, and other species in the North Sea and the North Atlantic and North Pacific oceans. As with the great whales (see "Whaling," p. 194), fishing effort in these fisheries has long surpassed the optimal catch. Overfishing is by far the biggest threat for fish species listed as endangered or vulnerable to extinction. The traditional major fishing areas of the world are not the only ones becoming exhausted. Small-scale local fisheries in the tropics, where most people live and where food is needed the most, are being rapidly decimated.

Most of the world's fisheries are already fully exploited, and at least a quarter or more are overexploited or even exhausted.

The danger of overfishing can be particularly serious in herrings, anchovies, and other clupeoid fishes. These species often undergo dramatic population cycles and may therefore be especially vulnerable to fishing pressure. This is the situation in the Peruvian anchovy, or *anchoveta* (*Engraulis ringens;* see "Of Fish and Seabirds, Fishers and Chickens," p. 389).

Overfishing is threatening many other species, particularly large fishes such as tunas, swordfish, and sharks. Recent studies have shown that around 90% of the biggest fishes in the world oceans are already gone, taken by big commercial fishing fleets. Only around 10% of the original stocks remain. The fish that now remain are also smaller than before the intensive fishing started, an average of half the size 20 years ago in the case of tunas. Small females produce less eggs than large females, and, at least in some species, larvae from small females are smaller and grow slower than larvae from larger females.

The disappearance of the most valuable fishes, which happen to be higher in the trophic pyramid, has forced fishing lower on the pyramid. Such a shift may cause unknown changes in the whole ecosystem, such as an increase in the number of non-utilized plankton or in undesirable predators like jellyfishes and comb jellies.

Bigeye tuna (*Thunnus obesus*) were about two times as heavy and eight times more abundant in the 1950s than at present. The northern bluefin tuna (*Thunnus thynnus;* see Fig. 1.18), among the largest of bony fishes and the most valuable (*sashimi* and *sushi* lovers have been known to pay as much as $770 per kilogram, $350 per pound, in Tokyo) has fallen by 90% since 1970 in the western Atlantic. It was not until 1995 that nations agreed to cut their catches in half, which many fisheries scientists regard as too little, too late.

Sharks, slow to grow and reproduce, have critically declined in many parts of the world. A 2002 study showed that populations of most species of sharks along the eastern coast of the United States had declined by at least 50% from the previous 15 years.

Another prized food fish, the swordfish (*Xiphias*), has also been victim of overfishing. North Pacific populations fell approximately 70% between 1960 and the late 1990s, and most of the fish caught by U.S. fishing boats were caught before they were old enough to reproduce. Fisheries that targeted swordfish closed in large areas of U.S. waters in the Atlantic and Gulf of Mexico. Longline fishing for tuna was closed in some areas because many swordfish are caught and killed on longlines. There is evidence that these measures have worked, and the number of swordfish in the North Atlantic is on the increase and perhaps on a road to recovery.

Damage to habitats is another threat to fishery resources. Estuaries, mangrove forests, seagrass beds, and other threatened environments are critical breeding grounds and nurseries for fishes, lobsters, shrimps, scallops, and other valuable species. Three-quarters of the commercial catch of the United States consists of species that inhabit estuaries during part of their life. Bottom trawls disrupt the sea floor, another form of habitat damage. Seamounts, inhabited by many unique species, are particularly vulnerable (see "Biodiversity in the Deep Sea," p. 375).

By-catch, organisms that are caught unintentionally while fishing for other species, is another problem. It is estimated that around 25% of the worldwide catch, roughly 25 million tons, is by-catch. A good portion of the by-catch, however, goes unreported. The swordfish caught and killed on longlines set for tuna are one example of by-catch; longlines also catch turtles, seabirds, dolphins, and other marine life. Trawling also produces a lot of by-catch. This is particularly true of shrimp fisheries, where as much as 95% of the total catch is by-catch because of the small size of the net's mesh. Some of the by-catch is kept but much of it is discarded. Even if it is released alive, most of the discarded by-catch dies. A large part of the by-catch in trawl fisheries is juveniles of valuable species sought in other fisheries, or worse, of protected species like cod in the Grand Banks. Yet another threat to fisheries is pollution from oil spills, sewage, and toxic chemicals. The effects of habitat destruction and pollution are examined further in Chapter 18.

The potential effects of overfishing on whales, seals, and other marine mammals that feed on fish are the subject of much debate and controversy. Conservationists see overfishing as a threat to the already endangered marine mammals, while fishers see protected marine mammals as a threat to their diminishing stocks. A 2004 study suggested that on a global scale marine mammals and fishers rarely prey on the same stocks. Significant overlaps between feeding by marine mammals and fishing, however, do exist in some regions.

Overfishing may be responsible for the destruction of kelp forests by sea urchins in the Aleutian Islands in Alaska. Because fish-eating seals and sea lions have become less common, killer whales that normally hunt them have turned instead to sea otters, which keep sea urchins under control (see "Kelp Communities," p. 296).

Of Fish and Seabirds, Fishers and Chickens

The ocean has been good to Perú. As the cold Perú Current flows northward, coastal upwelling (see Fig. 15.30) pumps nutrients from the depths in huge amounts. The resulting increase in primary production supports a rich harvest of plankton that in turn feeds immense schools of the Peruvian anchovy, or *anchoveta* (*Engraulis ringens*). This high productivity is a critical part of a complex cycle that has had tremendous consequences for the economy of Perú.

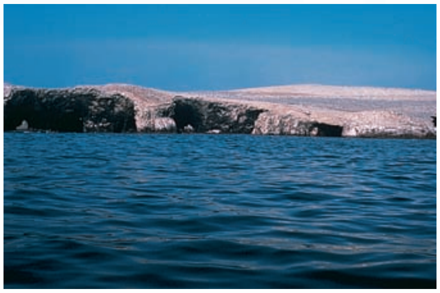
From time immemorial, clouds of cormorants, boobies, and other seabirds have gorged themselves on the anchovy schools. The birds roost and nest on small islands along the coast. With hardly any rain to wash them away, the birds' droppings slowly build up in the dry climate. Over thousands of years the droppings have accumulated into layers as thick as 45 m (150 ft). This thick crust, called **guano,** is rich in nitrogen and phosphorus and is an excellent fertilizer.

The fertilizer starts out thousands of miles away, when organic matter sinks from the surface to the depths of the Pacific. When the organic material decomposes, nitrate and phosphate, the main nutrients for phytoplankton, are released into the water. The nutrients remain in the dark depths, unavailable to phytoplankton, until upwelling eventually brings them into shallow water along Perú's coast. Here they are taken up by diatoms and other phytoplankton, which form the base of the food web. The plankton are eaten by the anchovies that feed the guano birds. Nutrients thus travel from the depths of the Pacific to the coastal islands of Perú with the help of upwelling, plankton, anchovies, and seabird droppings!

And then people came along. Guano, a valuable agricultural fertilizer, was mined and exported. The guano industry brought considerable wealth to Perú, and by the end of the nineteenth century millions of tons had been mined. What took thousands of years to deposit was used up in a matter of decades.

The anchovies were next. A commercial anchovy fishery was established in the early 1950s and grew to unprecedented dimensions. It became the world's largest single fishery and made Perú the largest fishing nation (Fig. 17.3). Catches continued to increase, except in years when El Niño, the warm currents that occasionally arrive at Christmastime, interfered with upwelling (see "The El Niño–Southern Oscillation Phenomenon," p. 353).

Immature boobies (*Sula*) on a Peruvian guano island.



Islas Ballestas, guano islands off Pisco, Perú.

Ironically, anchovies are so small that they are not often used for human consumption. Most of the catch was exported as fish meal for chicken feed. Fish meal from Perú became the world's single largest source of protein meal. Most of this protein was consumed by farm animals in other parts of the world, while many Peruvians continued to have protein-deficient diets.

By the late 1960s, the annual catch surpassed the estimated optimal, or maximum sustainable, yield of around 10 million tons a year. After the 12.3-million-ton catch of 1970, the fishery collapsed. The guano birds also suffered a dramatic decline. The El Niño of 1972 added to these woes.

The collapse had widespread effects. The price of other protein meals, particularly soybean meal, increased. In Brazil alone, several million acres of tropical rain forest were cleared to grow soybeans.

Another dramatic collapse of a fishery is that of the Pacific sardine (*Sardinops caerulea*), which supported a booming fishery in California until it crashed in the 1940s. The reasons for its collapse and that of the Peruvian anchovy are not entirely clear. Overfishing was not the only cause. Clupeoid fishes like anchovies and sardines naturally undergo population cycles. It may well have been that the combination of heavy fishing pressure and a dip in the natural cycle pushed these fishes over the brink. El Niño also enters into the picture. Harvest records since the beginning of the twentieth century show that, when the Peruvian anchovy was thriving, the Pacific sardine occurred in low numbers, and vice versa. Populations of these two Eastern Pacific species thus appear to have cycles that are opposite to each other for reasons that are not very clear. It has been speculated that warm water in the Pacific due to a strong El Niño translates into high sardine and poor anchovy harvests; cool water and a weak or absent El Niño bring high anchovy, poor sardine harvests. It is obvious that management of fisheries for species like the Peruvian anchovy needs to be tuned to the fishes' biology, with heavy fishing in some years and sharply curtailed harvests in others.

Since its collapse, annual catches of the Peruvian anchovy have varied from a low of 93,654 tons in 1983 to 9.8 million tons in 1994 (Fig. 17.3), becoming again the world's largest marine fish catch and making Perú the second-largest fishing nation. The 1997–1998 El Niño caused a 78% drop in the catch, to 1.7 million tons in 1998. It soon recovered, however, and by 2000 the catch was 11.3 million tons. It decreased to 6.2 million tons in 2003 but nearly doubled to 10.7 in 2004, the largest fishery in the world. Will the number of anchovy, and guano birds, eventually return to their former levels? Perhaps more important is whether any lessons have been learned. Will the same mistakes be repeated elsewhere?

A fishery is regarded as collapsed if catches fall below 10% of historic highs. Nearly one-third of all the species that are fished have already collapsed, and around 60% are predicted to collapse by 2025. A 2006 worldwide study by 14 marine scientists concluded that *all* of the world's fishing stocks will collapse by mid-century if no drastic measures are taken to curb overfishing, by-catch, destruction of habitats, and pollution.

Managing the Resources Given the danger of overfishing, most people agree that fisheries resources should be harvested in a way that does not deplete them beyond recovery. In other words, fisheries must be managed to ensure their long-term value. The wise management of fisheries stocks is much harder than it sounds. For one thing, the maximum sustainable yield can be very difficult to estimate. To do so, fisheries biologists need detailed information about the size of fisheries stocks, how fast the organisms grow and reproduce, how long they live, and what they eat (which often changes at different stages of the life cycle; see Fig. 15.24). Such information is rarely easy to obtain and often unavailable. Biologists may have to rely on rough "guesstimates" or questionable assumptions, making their estimates of the optimal catch less reliable.

Furthermore, real fisheries are much more complex than we have indicated. The smooth catch-effort curve shown in Figure 17.10 represents a greatly simplified model and does not take many natural features into account. For example, the harvested species may be **competing** with other species, and fishing pressure might alter the competitive balance. Schools may get smaller as a result of fishing. This might not only make the fish harder to catch but also adversely affect their behavior and reproduction. Simple models do not consider the size of the fish caught, but it makes a difference whether large, older individuals or small, younger ones are caught, for example, because large individuals typically produce many more eggs than small ones. Similarly, the time of year when fishing is done may be important, such as whether the catch is taken before or after the breeding season. These natural complexities can have dramatic consequences and could cause a fishery to fail unexpectedly if not taken into account.

Given the uncertainties of determining optimal catches and the disastrous effects of overfishing, it can be argued that the catch should be set somewhat lower than the estimated optimum just to be on the safe side. A fisher, however, with a family to feed and boat payments to make, might have different ideas. The same can be said of cannery and dockyard workers, gear merchants, bankers, and all the other people who depend directly or indirectly on the fishery. Thus, fisheries management is a complex, often controversial, matter that is affected by economic and political factors as well as biological ones. If the catch is harvested by more than one nation, international relations also come into play.

Once a desired catch level is agreed on, there are a number of ways to manage the fishery. The total catch may be limited by closing the season as soon as the target catch is reached or by restricting the length of the season, the number of boats or fishers, or the areas open to fishing. The size and power of boats can be limited or certain methods of fishing can be banned altogether. Limits can be placed on the catch of each boat or, if an international fishery, each nation. By regulating the mesh size of nets, fishers may be prohibited from taking individuals of certain sizes (Fig. 17.11). Leaving the largest individuals to reproduce can help in the recovery of overfished stocks. If sexes can be told apart, fishers may be prohibited from taking females.

The total collapse of once thriving fisheries has sometimes forced the use of drastic measures. Governments may reduce their fishing subsidies, they may pay fishers to give up fishing, or a fishery may be closed altogether. Complete closures, however, are in effect in less than 1% of the world's fishing grounds. The establishment of reserves or sanctuaries to preserve important habitats is another possible way to safeguard the survival of important species, perhaps allowing the species to repopulate outside areas that are open to fishing.

Besides preventing overfishing, management measures may be undertaken to help restore stocks that have become depleted. These measures may involve the improvement and protection of essential habitats or the transplantation of artificially raised young.

The management of fisheries to prevent overfishing includes the establishment of quotas, restrictions on the type of fishing gear, and other measures.

Fishing rights over a nation's territorial waters are a complicating factor in the management of resources. Traditionally, a country's territorial waters extended 3 nautical miles (5.5 km) offshore. Some nations, however, began to exclude fishing fleets from other nations by extending their territorial waters. Fishing disputes even led to wars. A general compromise was finally reached in 1982 with the **United Nations Convention on the Law of the Sea** (**UNCLOS;** see "Prospects for the Future," p. 427), which so far has been ratified by 149 nations. It allows nations to establish an **exclusive economic zone (EEZ)** 200 nautical miles (370 km) offshore. Within this zone, nations can completely control their fisheries, oil, and mineral resources. Nations are required to use their resources in a sustainable way. They can keep foreign

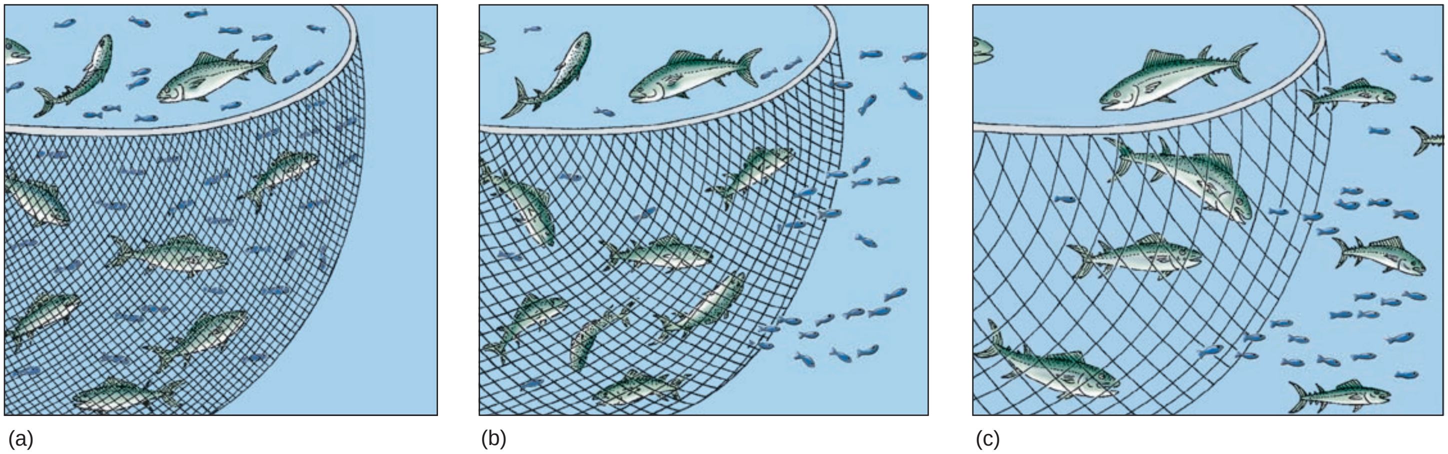

(a) (b) (c)

FIGURE 17.11 Both the size and species of fishes caught by nets can be controlled by the net's mesh size. (*a*) A fine net might catch both sardines and tuna. (*b*) With a larger mesh size the sardines escape and only tuna are caught. (*c*) With an even larger mesh size only large tuna are taken.

fishers out if they wish or sell fishing licenses to foreign fleets. EEZs cannot always be policed, of course, and foreign fishers may sneak in and fish without permission or with illegal gear. When caught, these pirate vessels are usually impounded.

The establishment of an exclusive economic zone (EEZ) allows nations to protect fishing and other resources 200 nautical miles around their shores.

In the United States, which has not yet signed UNCLOS, the Magnuson-Stevens **Sustainable Fisheries Act** of 1996 required federal fisheries managers to develop management plans to prevent overfishing, restore depleted stocks, and reduce by-catch, the first time protection has been extended to non-commercial species. Vessels of foreign nations that have signed fishing agreements with the United States are allowed to fish in U.S. waters only after receiving a fishing permit. The 2003 **Pew Oceans Commission** went further than the Sustainable Fisheries Act by calling for a reform of the nation's ocean laws and policies to protect marine ecosystems. This independent commission recommended a unified policy to restructure fishery management to ensure not only sustainable exploitation but also the protection of whole ecosystems. It stressed the need to regulate fishing gear that harms the marine environment, the monitoring of by-catch, and the control of pollution caused by mariculture.

More than 90% of the ocean's present fisheries, however, lie within the EEZ of one nation or another, but the high seas are still considered common property. A number of potential new fisheries lie outside territorial boundaries and thus are open to all nations.

Efforts toward the better management of resources have already brought about some positive results. A limited number of fisheries in a few countries are now being successfully managed. Fish from these sustainable fisheries are "eco-labeled," so that consumers can select it over fish from overexploited catches. It is hoped that this marketing strategy will also encourage calls for better fisheries management of overfished stocks.

New Fisheries Fisheries scientists have for decades been absorbed with the possibility of tapping new or underexploited fisheries. One possibility is to increase the use of by-catch. The main problem with much of the by-catch is not so much that there is anything wrong with it but that people simply will not buy it. Consumer tastes are fickle and vary from place to place. What is considered a delicacy in one place is junk in another. Hake (Table 17.2), for instance, is prized in Europe but not in the United States. Croakers and sea robins are common throwaway fishes in the United States that are eaten elsewhere. Squids are caught in large numbers in California, but most of the catch is exported, primarily to Japan. Squids are a delicious source of lean protein, but American consumers were suspicious of the sucker-armed molluscs, though marketing squid by its Italian name of *calamari* has increased its appeal. A name change also helped overcome consumer resistance to eating dolphinfish (*Coryphaena hippurus*), certainly a fish and not a dolphin. The more seductive Hawaiian name of *mahimahi* helped enhance its marketability.

A potential use of the by-catch is to process it into products that have more market appeal. In the *surimi* process, for example, low-value fish is washed to remove fat, minced, and mixed with flavorings and preservatives. Appropriately shaped, it is sold as imitation crab, lobster, shrimp, or scallop. Alaskan pollock is now the main component, but less desirable fish species could also be used. Processed fish products such as fish sticks could also open the market to less popular catches. Unwanted catches could also be converted into fish flour and used to protein-enrich all sorts of processed foods.

The highly productive waters around Antarctica are often mentioned as potential sources of increased commercial catches. Antarctic catches include various fishes, squids, the southern king crab, and krill (Fig. 17.12). Even in the harsh conditions of Antarctic waters, however, overfishing is taking its toll. The waters around South Georgia Island, for instance, are already overfished. The Patagonian toothfish (*Dissostichus eleginoides*), marketed as "Chilean sea bass" in the United States, has been seriously depleted,

Competition When one organism uses a scarce resource at the expense of another.
- Chapter 10, p. 213

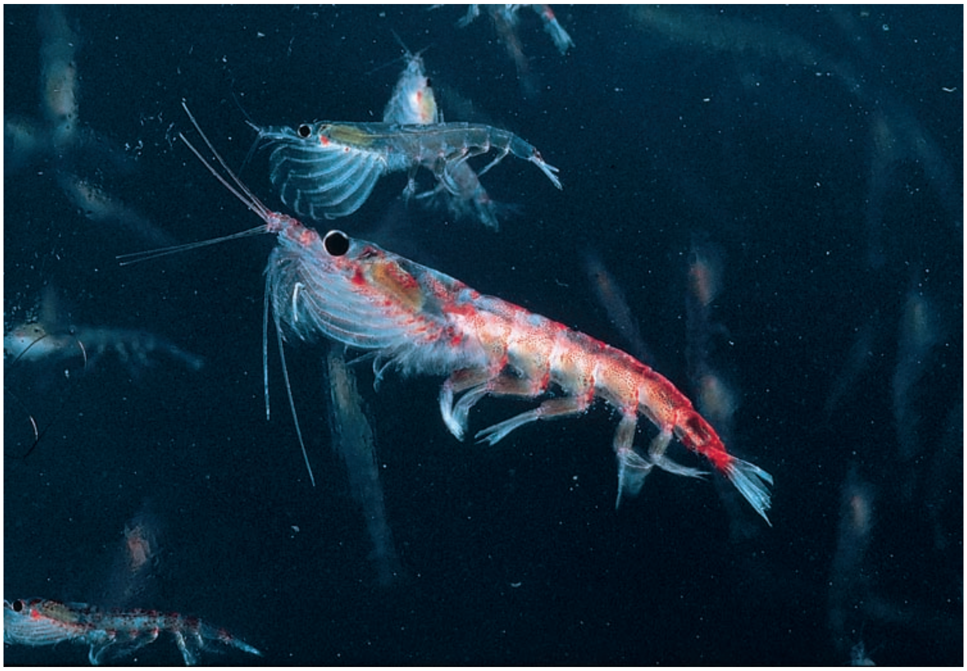


FIGURE 17.12 Krill (*Euphausia superba*) form dense schools in Antarctic waters and were thought to be potential human food. Predictions of annual catches in the millions of tons, however, have not yet materialized.

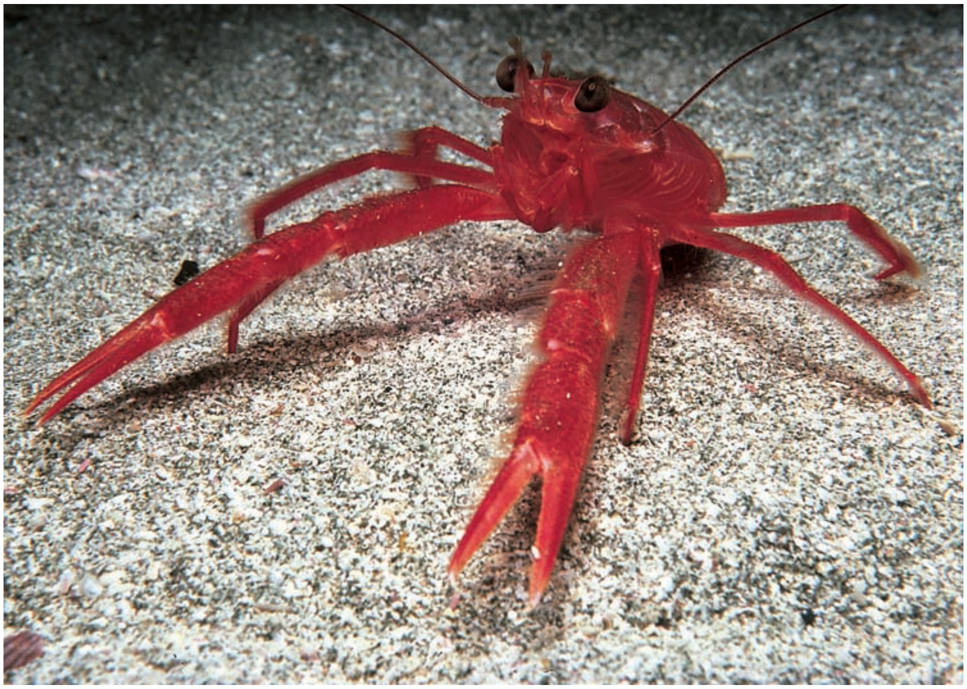


FIGURE 17.13 *Pleuroncodes planipes,* also called the lobster krill or tuna crab, is a pelagic crab that has been suggested as a potential source of human food. Large swarms of the crab, each having a maximum length of 13 cm (5 in), are often washed ashore on the Pacific coast of California and Mexico, turning beaches bright red. A possible problem with this plan is that *Pleuroncodes* is an important food for tunas.

mostly by illegal fishing. Many illegal fishing vessels operate under flag-of-convenience countries that may not enforce international maritime law. Illegal longline fishing has also affected populations of seabirds, especially albatrosses (see "Threatened and Endangered Species," p. 413).

There are other potential sources of food from the sea. Some of these are underutilized. Others are unconventional species like squid and other cephalopods, flying fishes, and pelagic crabs (*Pleuroncodes;* Fig. 17.13). Lanternfishes (*Myctophum;* see Fig. 16.6) represent another potential fishery. They are found in deep water but migrate to the surface at night in the **deep scattering layer.** They form dense schools in most oceans. These and other species remain underexploited or completely unexploited mainly because of lack of consumer acceptance or the absence of efficient fishing methods. Some may eventually support successful fisheries, though probably for fish meal rather than for human consumption.

Measures to increase the supply of food from the sea include an increase in the exploitation of underutilized species and the development of new fisheries.

Mariculture Instead of overfishing the dwindling natural food resources of the oceans, why not raise marine organisms as we do farm animals? This is not a new idea. The Chinese have been doing it with freshwater fishes for thousands of years, the Romans farmed oysters, and the early Hawaiians built walled fish ponds along the coast to raise mullet (*Mugil*) and milkfish (*Chanos chanos*). The application of farming techniques to the growth and harvesting of marine organisms is known as **mariculture,** the agriculture of the sea. A more general term is **aquaculture,** which is applied to the farming of both freshwater and marine organisms. The worldwide culture of marine fish and shellfish alone reached 18.3 million metric tons in 2004, with an estimated value of $28.9 million. These figures, more than three times the volume and more than twice the value of those in 1990, show the rapid growth of mariculture (see Fig. 17.3). The 2004 figures are higher if the culture of seaweeds (13.9 million metric tons with a value of $6.8 million) are included. The culture of freshwater animals in 2004 was 27.2 million tons, with a value of $34.5 million. Aquaculture has also grown more than three times faster than livestock production on land, and according to FAO aquaculture is the world's fastest-growing food-production sector. Approximately 34% of all the fish consumed around the world is farmed, although this is mostly freshwater fish. The growth of fish farming averaged 11% a year during the 1990s, and the output for 2010 is predicted to be higher than cattle ranching around the world. Shrimp mariculture showed tremendous growth, with an increase in volume of more than 300% from the mid–1980s to the early 2000s. Farmed shrimp now account for around 25% of the estimated 3 million tons of shrimp consumed every year around the world. Though mariculture is used primarily to grow food species, it is also used to grow commodities such as cultured pearls (see "Bivalves," p. 130) and fishes for the aquarium trade.

Mariculture is the farming of the sea for food and other resources. The term "aquaculture" includes the culture of freshwater species as well.

Traditional mariculture is still practiced in several parts of the world, particularly in Asia. Milkfish is farmed in ponds filled with brackish water, that is, partially diluted seawater (Fig. 17.14). The immature fish, or fry, are captured from the wild, transferred to the ponds, and fed with agricultural by-products. In this way, wastes are converted to fish flesh that is cheaper to produce than pork or beef. These fish farms provide not only high-protein food but jobs as well.

With various modifications, similar operations are used to farm other fishes, molluscs, shrimps, and seaweeds in many parts of the world. The fry or spat (immature bivalve molluscs) are transplanted to favorable sites in coves (Fig. 17.15), natural ponds, estuaries (including fjords), and mangrove forests. Already, shrimp mariculture is a significant source of foreign exchange earnings for several developing countries. Salmon and other fishes are raised in large floating pens or cages. Pacific threadfin, or *moi* (*Polydactylus sexfilis*), and others are raised in giant cages submerged off Hawai‘i. Oysters, mussels, and other

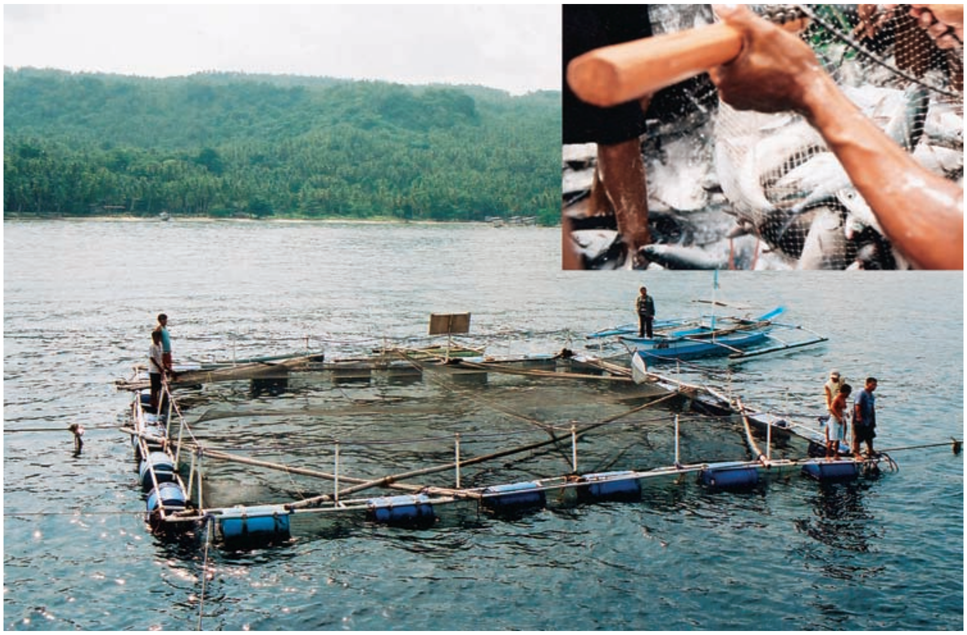


FIGURE 17.14 Milkfish (*Chanos chanos*) is harvested from floating cages and brackish-water ponds in the Philippines. Some will be eaten, others allowed to mature and spawn to replenish the cages and ponds.

molluscs are grown on racks, in baskets, hanging from rafts, and in other ingenious ways. This type of mariculture, in which farming takes place under more or less natural conditions with relatively little manipulation by humans, is known as **open mariculture,** or **semi-culture.**

Sometimes, however, the farming of high-value food species is a different story. In what can best be described as the domestication of marine organisms, growth is maximized by almost totally controlling the organisms and their environment. This type of mariculture is called **closed,** or **intensive, mariculture.**

Intensive mariculture poses many problems, and only a small percentage of marine food species can be farmed (Table 17.3). Species like clupeoid fishes and tunas that require large, open spaces are not good candidates for intensive mariculture. To be farmed successfully, most species need specialized sites and equipment. Water pumped into tanks, pools, or other holding facilities must be free of pollutants and carefully checked for temperature, salinity, and other chemical factors. Toxic wastes from the organisms themselves must also be removed. Food can be a problem because the various stages of a species usually have different food requirements. This is a particular problem when trying to culture planktonic larval stages because they require specially cultured food. Predators and disease-causing organisms must be periodically removed or killed. Parasites and disease can be devastating under the crowded conditions typical of culture operations (see "Effects of Farmed Salmon on Wild Salmon Populations," p. 396). Viral infections are a serious problem in shrimp farming. Even sneaky seabirds and sea lions have learned to help themselves to the precious fish that are raised so painstakingly. Crowded conditions tend to cause cannibalism among fishes and crustaceans. Juvenile American lobsters, for instance, must be kept apart or they eat each other. Commercial mariculture, however, is a challenge that many enterprising, business-oriented fisheries scientists are willing to accept. It is now possible, for example, to freeze shrimp sperm, ensuring year-round reproduction. We have learned to induce the settlement of the planktonic larvae of abalone, a valuable mollusc. Scientists can even create oysters with three sets of chromosomes, instead of the normal two. This makes them sterile. Normal oysters develop a strong taste when their eggs mature, but sterile ones, which do not produce eggs, are always tasty.

Rather than raising them all the way to harvest, some species are grown for only a short time, then released as fry or juveniles to enrich natural populations in a process known as **seeding.** Salmon are an interesting example of seeding. In some places, especially Europe, salmon are held in captivity their entire lives, from hatching to harvest. In other places the salmon are released as juveniles to feed and grow at sea. Several years later they return as full-grown adults to the stream where they were released. Not only can they be caught by commercial and sport fishers in the usual way, but they swim right back to the hatchery,

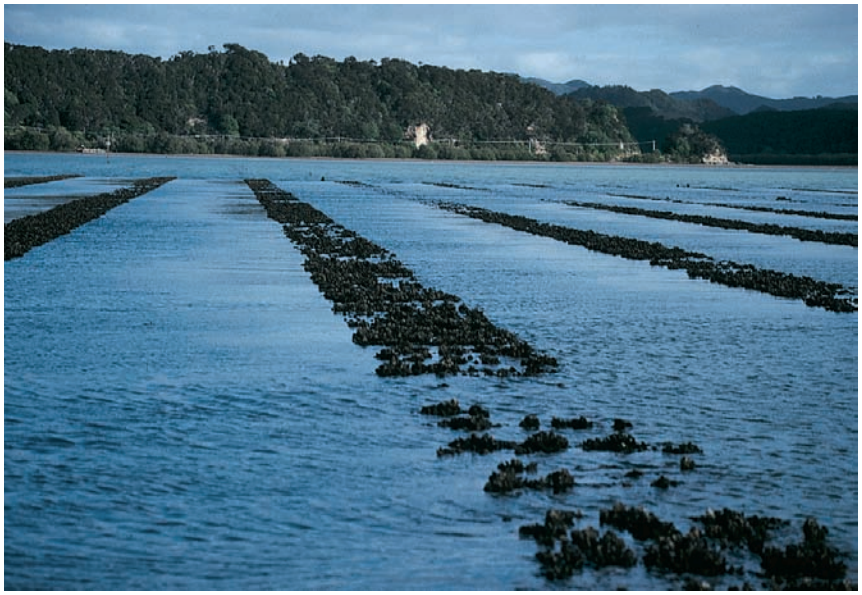


FIGURE 17.15 The farming of oysters (*Crassostrea glomerata*) in Whangaroa, New Zealand.

Deep Scattering Layer Animals, mostly fishes and shrimps, that migrate vertically between the mesopelagic and epipelagic zones.
- Chapter 16, p. 364

Table 17.3 Examples of Marine and Brackish-Water Species Used in Commercial Mariculture

Species Cultured	Major Areas Where Cultured
FISHES	
Atlantic salmon (*Salmo salar*)	U.S., Canada, Chile, Europe
Bluefin tuna (*Thunnus thynnus*)	Japan
Cod (*Gadus*)	Europe
Flatfishes (*Solea* and others)	U.S., Europe
Horse mackerel (*Trachurus*)	Japan
Milkfish (*Chanos chanos*)	Southeast Asia
Mullets (*Mugil*)	Southeast Asia, Mediterranean
Pacific salmon (*Oncorhynchus*)	U.S., Canada, Chile, Japan
Puffer (*Fugu*)	Japan
Red seabream (*Pagrus major*)	Japan
Yellowtail (*Seriola*)	Japan
MOLLUSCS	
Abalone (*Haliotis*)	U.S., Japan
Clams, cockles (*Anadara* and others)	Southeast Asia
Mussels (*Mytilus, Perna*)	U.S., Europe, New Zealand
Oysters (*Crassostrea, Ostrea*)	U.S., Europe, Japan, Taiwan, Australia, New Zealand
Scallops (*Pecten, Patinopecten*)	Europe, Japan
CRUSTACEANS	
Shrimps (*Penaeus* and others)	U.S., Ecuador, Mexico, Japan, China, Southeast Asia, India, Bangladesh
SEAWEEDS	
Red (*Porphyra, Eucheuma*) and brown (*Laminaria*) algae	Japan, China, Southeast Asia, South Pacific

where the ones not used for breeding can be caught and harvested. This practice, known as **salmon ranching,** originated in the Pacific Northwest of North America but has been transplanted to locations as far away as Chile and New Zealand.

Most mariculture operations require expensive equipment and specialized personnel. These demands further restrict the number of species that are cultured: Some species that could be farmed are not because it is not profitable. Species that are cultured are usually those that command high prices. Thus, instead of mass-producing cheap protein for a hungry world, mariculture tends to provide variety in the diet of the affluent.

Another drawback of mariculture is pollution. Fish farming in which thousands of fish are concentrated in ponds along the coast or in extensive floating pens releases huge amounts of feces, urine, and uneaten food that ultimately degrade water quality. The decomposition of these wastes depletes oxygen in the water and releases nutrients that can trigger harmful algal blooms. Farmed fishes also concentrate toxic chemicals.

Some fish farms also use chemicals like antibiotics, pesticides, and synthetic pigments, which may be harmful to surrounding marine life. Another risk is the introduction of parasites and diseases to local marine species in the wild. Even more devastating can be the destruction of the natural environment. Clearing for shrimp farms, for example, has caused the destruction of mangrove forests, salt marshes, and other coastal communities in the tropics and subtropics (see “Human Impact on Estuarine Communities,” p. 281). This destruction has reduced the stocks of local species that use mangrove forests and salt marshes as nurseries. Though shrimp is a more profitable product, less food is actually produced than in the destroyed environments. Introduced farmed species that escape are potentially harmful to native species and the communities they live in, and catching fish from the wild to feed farmed fish, a common practice, may also deplete wild fisheries. Escaped Atlantic salmon breed with wild populations and dilute the **genome** of the wild populations, perhaps making the offspring more vulnerable to diseases and other natural stresses.

Still, some fisheries scientists and economists are optimistic. They predict that someday intensive mariculture will provide a significant amount of relatively cheap food. They pin these hopes on the development of technological improvements and fast-growing varieties of food species, and even turning carnivorous fishes into vegetarians that are much cheaper to raise. Other options are pumping nutrient-rich water from the deep sea to provide better culture conditions (Fig. 17.16), or from sewage discharges and use it to grow the planktonic algae that are fed to the larvae of fish and other species. The application of **genetic engineering** and other forms of **biotechnology** to mariculture is another possibility. Genetic engineering may soon allow scientists to alter the genetic information contained in a species’ **DNA** to produce faster-growing, more disease-resistant, or better-tasting strains. There is great concern, however, about the effects of escaped organisms that breed with wild populations.

Marine Life as Items of Commerce and Recreation

The living resources of the sea are used in many ways other than food. Timber and charcoal are obtained from mangroves. Jewelry is made from pearls, shells, and black and precious corals and leather from the saltwater crocodile (Fig. 17.17), sea snakes, sharks, and other fishes. Many of these resources, however, are being overexploited. Rich mangrove forests are being rapidly cleared, and black and precious coral have disappeared in many areas. Many endangered species are taken. Fur seals, for example, are killed for their pelts, and hawksbill turtles are taken for tortoiseshell.

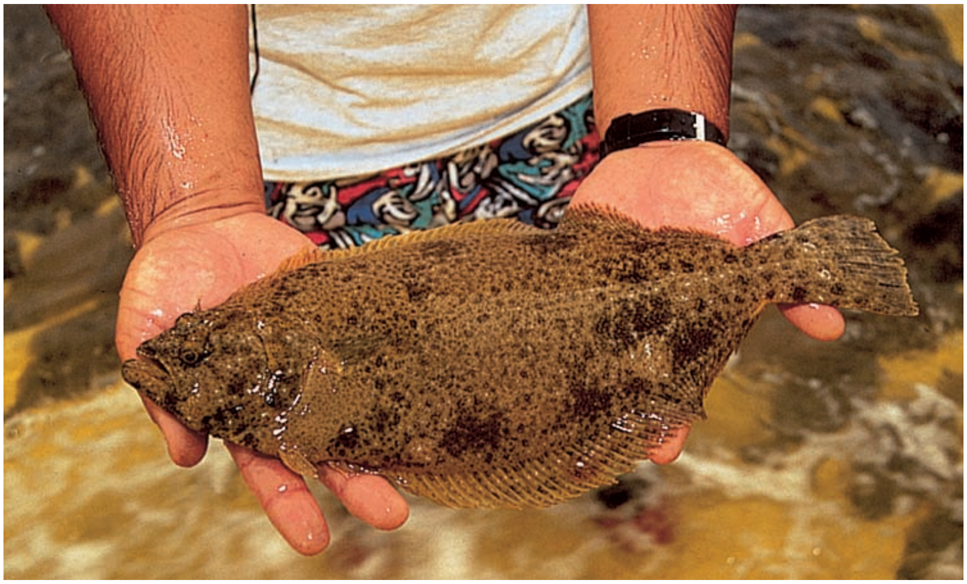


FIGURE 17.16 A Japanese flounder, or bastard halibut (*Paralichthys olivaceus*), grown at a mariculture facility in Hawai'i. This operation uses cold, nutrient-rich water that is pumped from a depth of 600 m (2,000 ft) not just to raise fish but mainly to generate power. The flounder, or *hirame,* commands high prices because it is highly sought for raw fish dishes such as *sashimi.*

Chemical compounds that are obtained from marine organisms, or **marine natural products,** have potential for use in medicine. The medicinal use of marine natural products by the Chinese probably goes back a few thousand years, but such use in the West has been limited. Recent years, however, have seen an upsurge in the collection, analysis, and testing of new material. Seaweeds provide chemicals that are widely used in food processing, cosmetics, plastics, and other products (see "Economic Importance," p. 109). The search for drugs from the sea has become one of the most interesting branches of marine science, combining the fields of biology, chemistry, and pharmacology (see "Take Two Sponges and Call Me in the Morning," p. 397).

For millions, the living resources of the sea provide not a livelihood but relaxation, an ideal way to spend leisure time (see "Oceans and Recreation," p. 426). Recreational anglers catch everything from lobsters to big-game fishes. In the United States the marine recreational catch is estimated to be around 30% of the commercial catch of food fishes. Marine recreational fisheries are the basis of a multibillion-dollar business worldwide. Recreational fishers buy boating and fishing equipment and travel long distances to pursue their hobby, supporting the tourist trade. There is a growing conservation ethic among the recreational fishing community, which in many places is a powerful political voice for conservation. Still, recreational fisheries can exert tremendous pressure on fish stocks and therefore need to be carefully managed. They account for 23% of the catch of overexploited marine fish species in the United States, and for some species the recreational catch is larger than the commercial catch. Large predators, stocks of which are mostly depleted, are prime targets.

Business and fun are also combined in the thriving **aquarium trade.** Though the aquarium hobby is dominated by freshwater fishes, marine aquaria enjoy much popularity. The export of colorful marine tropical fishes such as lionfishes, butterflyfishes, and damselfishes is a significant component of trade in countries like the Philippines and Fiji. The aquarium trade has now extended to other tropical marine organisms: sea anemones, corals, sea urchins, and just about anything else that is colorful and might carry a price tag. Even "live rocks," rocks with their associated marine life, are sold.

The unrestricted and indiscriminate collection of marine life for the aquarium trade can be very destructive to the natural environment (see "Modification and Destruction of Habitats," p. 402). In the Philippines and other places aquarium fish are often collected by using poisons or explosives that kill hundreds or thousands

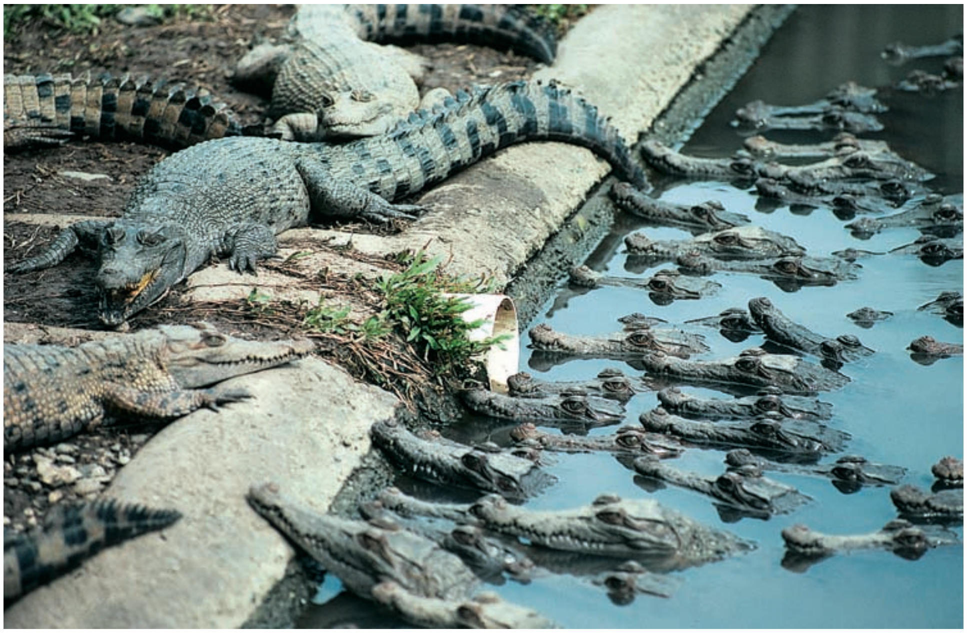


FIGURE 17.17 Saltwater crocodiles (*Crocodylus porosus*), here grown together with freshwater crocodiles (*C. novaeguineae*), are farmed in Papua New Guinea for their valuable skin. This farm was set up as a way to dispose of chicken offal from a chicken farm and earn some money in the process. Saltwater crocodiles are worth more than their freshwater cousins because they have smaller scales and therefore more of the skin can be used. They are harvested when they reach approximately 1 m (3 ft) in length.

Genome The complete genetic information of an organism.

DNA Nucleic acid that contains the cell's genetic information.

- Chapter 4, p. 65

EYE ON SCIENCE

Effects of Farmed Salmon on Wild Salmon Populations

Farmed salmon has become an important food item in developed countries, where it meets increased consumer demand for fish rich in protein and omega-3 fatty acids. Farmed salmon is cheaper than wild salmon and by now most salmon consumed, especially Atlantic salmon (*Salmo salar*), is farmed. The impact of salmon farming on the natural environment, however, has been the subject of much debate. Salmon farming releases pollutants and potentially harmful chemicals, farmed salmon has generally been found to contain higher amounts of PCBs and similar toxic chemicals than wild salmon, and the breeding of escaped salmon with wild populations may have risky long-term effects (see "Mariculture," p. 392).

Research undertaken in Europe and North America has revealed another type of potentially harmful effect. Results strongly suggest that populations of wild salmon and other fishes could be seriously affected by parasites that are common in farmed salmon. One particular culprit is sea lice (*Callous, Lepeophtheirus*), small copepods that as adults live on salmon and other fishes, where they feed on skin, mucus, and blood. Free-living larvae hatch from eggs that are carried by the parasitic females in two ribbon-shaped sacs. The larvae develop in the plankton and eventually molt into copepodite larvae (see Fig. 7.39) that are adapted to infest fishes. These small, immature stages feed on skin cells and may cause considerable damage to their fish hosts.

Sea lice are normally found on adult wild salmon, which lives at sea. When the fish returns to fresh water to spawn, however, the parasites drop off the fish because sea lice cannot tolerate fresh water. The small, immature salmon, which are born in rivers and migrate to sea (see "Migrations," p. 168), normally have relatively few lice, if any, since they rarely encounter adult salmon, which live far out at sea, during their migration. In contrast, sea lice have become a major pest of farmed salmon, which is raised through its complete life cycle in crowded floating pens along the coast. The parasite is responsible for millions of dollars a year in losses to fish farmers.

Research on the North Sea off Norway has shown that, in two fishes related to salmon, the sea trout (*Salmo trutta trutta*) and the Arctic char (*Salvelinus alpinus*), high lice infestation (over 100–200 lice larvae per fish) was present in populations close to coastal areas where there is extensive salmon farming, while populations in a region with little farming showed significantly lower infestation (few fish with more than 10 lice larvae), which appeared to be the normal infestation rate. Mortality was high in heavily infested fish.

More recent work in British Columbia on the Pacific coast of Canada by a team of scientists, including specialists in mathematical biology, showed similar results. The scientists tracked the migration of juvenile salmon past salmon farms to see where infections began and how they progressed. They then used mathematical models of parasite dispersal and fish migration to analyze the data and estimate the transmission of sea lice from farm to wild salmon and the subsequent decline in salmon survival.

Immature pink, or humpback, salmon (*Onchorynchus gorbuscha*) and chum, or dog, salmon (*O. keta*) were found to be rarely infected with sea lice before they passed a salmon ranch down two narrow corridors on their way to the open sea. Infestation was much higher in immature fish that had migrated past fish farms. Mortality was high, estimated high as 95% of the migrating fish, due to the fact that the small and fragile immature fish are easily harmed by a high load of lice.

The initial research raised many additional questions that lead to research in progress. Do other species of farmed fish have the same effect on wild populations, particularly those that migrate like salmon? Is the incidence of parasites other than sea lice also being increased by the effect of fish farming? Can a vaccine against sea lice infestation be developed and used to control the parasite among farmed fish? The wild stocks of other species of salmon and related fishes have shown alarming declines in recent years. How important is the effect of increased parasite infestation due to fish farming in relation to other potential factors unrelated to fish farming? What factors may be involved?

For more information, explore the links provided on the Marine Biology *Online Learning Center*:

of fish for every one that makes it to the neighborhood pet shop. The management of aquarium-species harvests, however, has helped reduce the impact of collecting in Australia and a few other places by harvesting reef fishes in a sustainable way.

The fisheries resources of the ocean are used for recreation by millions around the world.

NON-LIVING RESOURCES FROM THE SEA FLOOR

In addition to its living resources, the sea contains many non-renewable resources, resources that are not naturally replaced, such as oil, natural gas, and minerals. These resources are much harder and more expensive to locate and exploit under the sea than they are on land. Not surprisingly, the sea's non-renewable resources went largely unused while supplies on land were plentiful. More and more, however, land reserves are running out, and we are turning to the sea floor for new sources.

Oil and Gas

Oil and natural gas were among the first of the sea's non-renewable resources to be used commercially. In the late 1800s it was discovered that some California oil fields extended well offshore beneath the seabed. The oil was extracted using oil rigs mounted on wooden piers that extended out from shore.

The offshore oil industry underwent tremendous expansion during the 1970s, when the high price of oil and gas made offshore drilling immensely profitable. Oil and gas production on the continental shelf now occurs in the Persian Gulf, the Gulf of Mexico, the North Sea, and in other areas on all continents

Take Two Sponges and Call Me in the Morning

Obtaining drugs from the sea is not an easy task. It involves a sharp eye, intuition, good luck, and lots of frustration. It means diving in awesome coral reefs as well as working countless hours in the chemistry lab.

Colorful attached invertebrates that live in coral reefs—sponges, soft corals, sea squirts—are good candidates for biomedical research. Though seemingly defenseless, these very visible, soft, attached animals are rarely eaten by hungry fishes or crabs. This fact suggests that they have some type of defensive mechanism. Many of these colorful invertebrates are known to produce unique chemical substances that make them taste bad or allow them to get rid of hostile neighbors, and these chemical substances may have properties that can be beneficial to humans as well.

Marine organisms of potential value as drugs are collected, frozen, and sent to the lab for analysis. Crude extracts using alcohol and other solvents undergo trials to test their ability to kill or inhibit the growth of bacteria (that is, to act as antibiotics), fungi, and viruses. Extracts are also tested for their effect on cancer cells and for their potential use as anti-inflammatory agents. Laboratory animals and cultures of cells or tissues are used in these trials. Any promising extracts are further separated and chemically identified. Chemicals with particularly promising properties are then used by pharmaceutical companies to develop new drugs. This process entails another long series of tests that ultimately includes rigorous clinical testing on humans.

Many biomedical products have already been obtained from marine organisms. Some red seaweeds provide laxatives or chemicals that kill viruses. Sponges and gorgonians are a rich source of natural products; some act as antibiotics, whereas others have anti-inflammatory or painkilling properties. A bryozoan (*Bugula neritina*) is the source of bryostatin, a promising drug in the fight against cancer. So is didemnin B from a Caribbean sea squirt (*Trididemnum*). Squalamine, which circulates in the blood of sharks, has antibiotic and antifungal properties. It is being tested for its ability to starve tumors by cutting off blood supply. Shark cartilage, however, has shown not to be effective against cancer, as some had claimed. A glue that is naturally produced by bacteria that live on rocks may be used in the future to seal wounds in the skin and delicate tissues of humans. Horseshoe crab blood is used to test for contaminant bacteria in vaccines, injections, and space probes. Sunscreens have been obtained from corals and an alga. The toxins, or poisonous substances, found in many marine organisms are also of potential value in medicine. Tetrodotoxin, the powerful toxin from certain pufferfishes and porcupine fishes (see "Symbiotic Bacteria—the Essential Guests," p. 90), for example, is used in Japan as a local anesthetic and as a painkiller in terminal cancer patients.

This sponge from coral reefs in Fiji (*Acanthella cavernosa*) contains a potent chemical that kills worms, including some human parasites. The chemical is being tested for its potential use as a drug. The sponges are cultured on ceramic plates tied to plastic netting.

Marine organisms are also used as remedies in Eastern medicine. Chinese traditional medicine, for instance, recommends red seaweeds for weight loss and for lowering cholesterol. Seahorse extracts are believed to strengthen the kidneys and the circulatory system, but as a result seahorses are rapidly becoming rare worldwide.

Many other marine organisms are being investigated as potential sources of drugs. Deep-sea bacteria and archaea, dinoflagellates, and seaweeds are cultured to study their antitumor capabilities. Compounds from sediment bacteria might be used to combat antibiotic resistance in bacteria that cause infections. Even bacteria that are normally found on the eggs of shrimps and other crustaceans are being targeted as sources of antibiotics and antifungal drugs. A gel from seaweeds is being investigated to prevent HIV infection. A toxin from cone shells, one of several known conotoxins, was recently approved in the United States for the treatment of chronic pain. Other conotoxins are undergoing clinical tests as painkillers and in the treatment of epilepsy and depression.

Marine natural products may eventually provide us with the long-awaited miracle drugs that will conquer cancer or AIDS. They are probably waiting to be discovered in the tissues of a sponge, sea cucumber, or sea anemone on a distant coral reef.

except Antarctica. A large percentage of the continental shelves around the world is considered a potential source of oil and gas. Drilling is now extending into deeper water beyond the shelf. The enormous economic potential of these reserves was one of the factors that prompted the establishment of EEZs to protect national interests.

The continental shelves are a major source of oil and natural gas.

Exploiting offshore oil and gas can be a difficult and costly operation, especially when the deposits lie many miles offshore as they do in the North Sea. Powerful currents, huge waves, and miserable weather compound the problems.

Overcoming these difficulties has been a major accomplishment of ocean engineering. Exploratory drilling is done from drill ships or partly submerged or elevated platforms that can be towed from place to place and anchored in position on the sea floor. Once oil or gas is found, huge steel or concrete platforms are erected and secured to the bottom to extract it (Fig. 17.18). Remotely controlled submarines are being used to build facilities on the bottom, which include pipelines to transport the oil or gas to terminals on land. Floating platforms now allow oil and natural gas to be extracted as deep as 3,000 m (10,000 ft).

Another potential source of energy from the sea floor is **methane.** Vast stores of methane, both as bubbles and in the form of frozen compounds, **methane hydrate** (or **clathrates**), have been found in deep water worldwide. It will be some time,

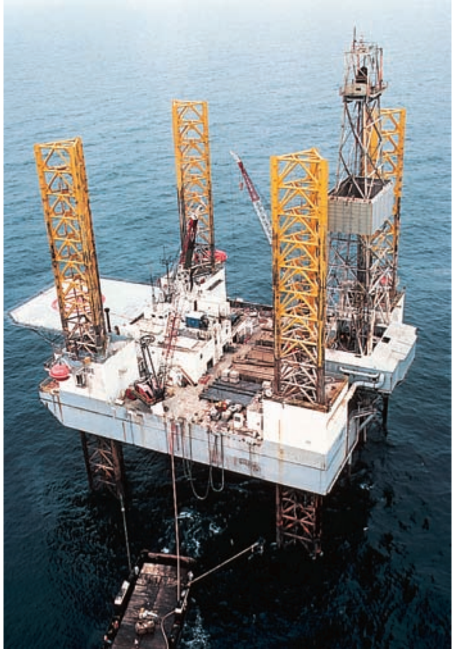


FIGURE 17.18 Oil-drilling rigs, like this one in the Gulf of Mexico off the Louisiana coast, are artificial islands built to cope with inhospitable conditions. They are serviced from land and incorporate the latest developments in undersea technology.

however, before the technology needed to exploit this resource is developed.

The potential threat of oil pollution, however, is a factor of great concern (see "Effects of Oil on Marine Life," p. 408). Pollution from drilling operations can affect coastal fisheries, tourism, and recreation. As a consequence, oil and gas drilling have been banned or strictly regulated in some coastal regions such as California.

Ocean Mining

The seabed is a potential source of many types of minerals; in fact, some people believe the bottom of the sea to be the planet's richest source. Though most marine deposits are not presently exploited, ocean mining will become more viable as we develop new technologies and as high-grade ores on land become exhausted.

Sand and gravel for the construction industry are mined along beaches and offshore in many parts of the world, exceeding quantities extracted on land. Sand is also extracted for its use in the glass industry. The galleries of some coal mines on land extend offshore underground. Some tin and even diamonds and gold are mined from offshore deposits brought to the seabed by rivers.

Among the most promising sources of minerals from the sea are offshore deposits of phosphates, which are widely used as fertilizers. Another potential source of minerals are **polymetallic nodules,** lumps of minerals that are scattered on the deep-ocean basins beyond the shelf. Polymetallic nodules contain manganese, nickel, copper, and cobalt, all of which are important to industry. Only a few areas have nodules with a mineral content high enough to make deep-sea mining economically feasible. Some of the richest deposits are found about 5,000 m (16,000 ft) deep in the equatorial Pacific south of the Hawaiian Islands.

Other mineral-rich sediments are found along the mid-ocean ridges and **hydrothermal vents.** The minerals are extracted from deep in the earth's crust as hot water percolates through volcanic fissures and vents. They are deposited when the hot water emerges and hits the cold ocean water. These deposits are rich in iron, copper, and zinc.

Polymetallic nodules and other mineral-rich deep-sea deposits are potential sources of valuable minerals.

There are many technical problems associated with mining the deep-sea floor. It is expensive, mainly because of the tremendous depths. The possible detrimental effects of mining on the surrounding marine environment have also been raised. The ownership of mineral resources that lie outside the EEZ is another unresolved issue. As metal prices rise, however, deep-sea mining may become more attractive. Several agencies and private companies continue to investigate the prospects of deep-water mining (Fig. 17.19). Future prospects include the use of specially designed dredges or suction pipes suspended from ships.

NON-LIVING RESOURCES FROM SEAWATER

Ordinary seawater, which contains a combination of many different **ions,** is a potential source of resources. It is certainly plentiful and easily accessible to coastal nations.

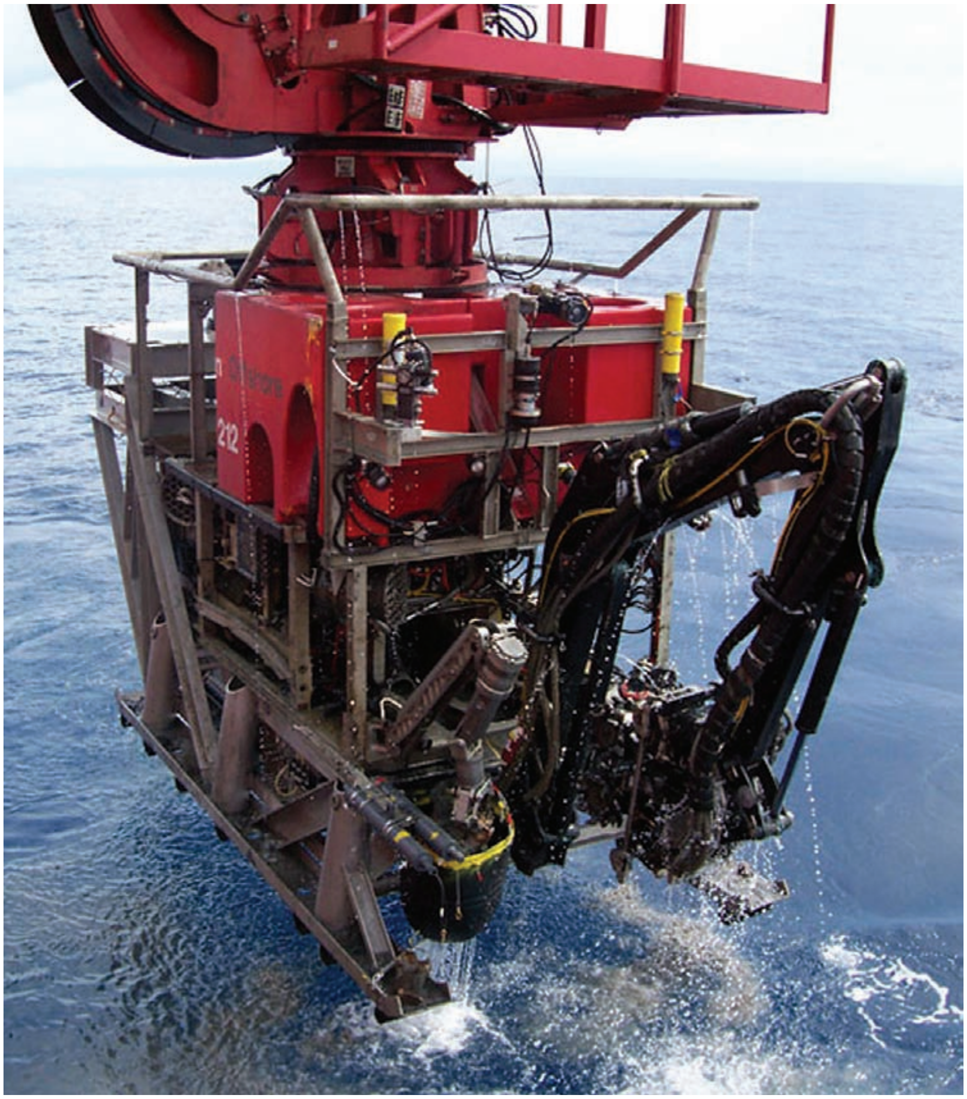
Fresh Water

Desalination plants that convert seawater into fresh water have been built in coastal regions that lack a sufficient supply of fresh water, mainly in desert and semidesert regions such as the Arabian Peninsula, Israel, and North Africa. Desalination is also used to supplement the water supply in densely populated areas like Hong Kong and Singapore, but it is extending around the world.

A few desalination systems are currently employed. The process of reverse osmosis, for example, uses a membrane that allows water to pass through but blocks the passage of ions, thus desalinating the water. Reverse osmosis plants are becoming very common in small-scale projects like resorts as well as in large desalination plants. Desalination, however, requires a great deal of energy and is therefore expensive. It also produces a highly saline residue that can cause environmental problems (see "Thermal Pollution," p. 413). New methods, perhaps using a renewable energy source like wind or wave power, may one day make desalination more practical and economical.

Minerals

Every element on earth is present in seawater, but mostly in extremely small quantities. The chief product presently obtained from seawater is **table salt,** or sodium chloride (NaCl), which is composed of the two most abundant ions in seawater, sodium and chloride. Salt, a precious commodity to ancient civilizations,



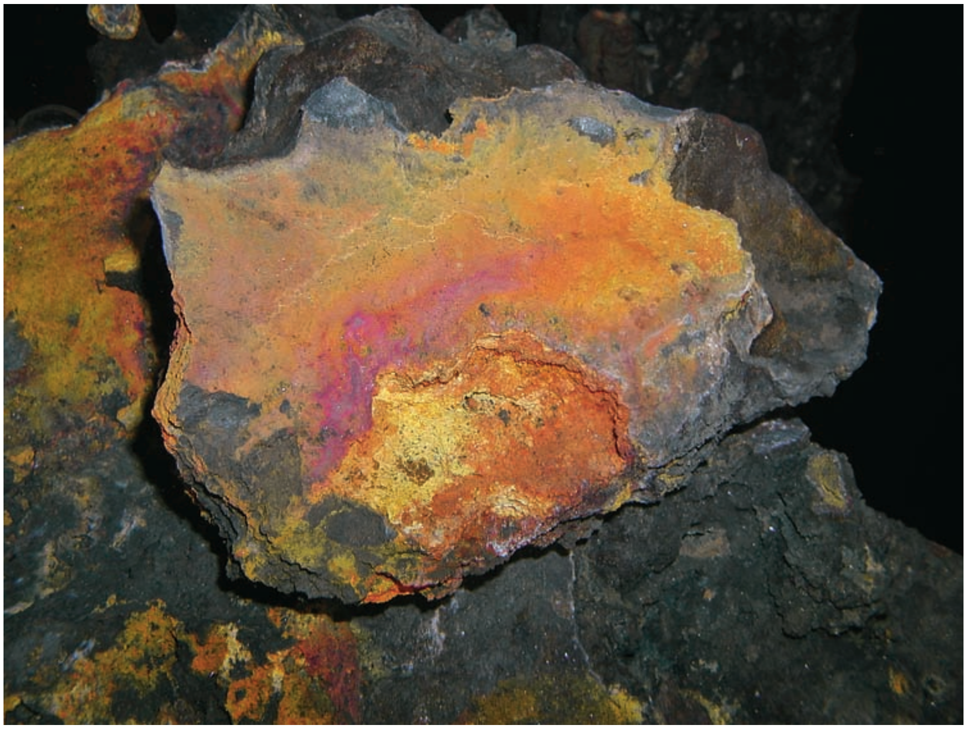


FIGURE 17.19 ROVs (remotely operated vehicles) are being used to commercially explore and sample the ocean floor off Papua New Guinea for minerals containing gold, silver, zinc, and, shown below in an underwater view, copper.

has been produced for centuries by evaporating seawater (Fig. 17.20). Most of the other constituents of seawater are difficult to extract because they are present in such small amounts (see Table 3.1, p. 44). Magnesium and bromine are also obtained from seawater in significant amounts, but valuable trace metals like uranium may one day be commercially extracted.

Seawater is a potentially rich but currently limited source of fresh water and minerals.

Energy

Most people don't realize that the ocean is a vast reservoir of energy that might be put to human use. Harnessing the sea's energy is the objective of several concepts that may help ease our dependency on fossil fuels and reduce CO_2 emissions.

Mill wheels have been used since ancient times to harness **tidal energy,** the tremendous energy contained in the normal ebb and flow of the tides. Modern schemes call for the construction of large barriers across narrow bays and river estuaries in areas where the **tidal range** is high, at least 3 m (10 ft). Water moving in with the high tide is caught behind the barrier, and locks are opened to release the water at low tide. The flowing water drives turbines that generate electricity from mechanical energy, just as in the hydroelectric plants in river dams. One such electrical generation plant has been operational

Hydrothermal Vents Undersea hot springs associated with the mid-ocean ridges encircling the earth, where new material is added to the earth's crust.

- Chapter 2, p. 37

Ions Charged atoms or groups of atoms that are formed when salts are dissolved in water.

- Chapter 3, p. 43

Tidal Range The difference in height between successive high and low tides.

- Chapter 3, p. 60

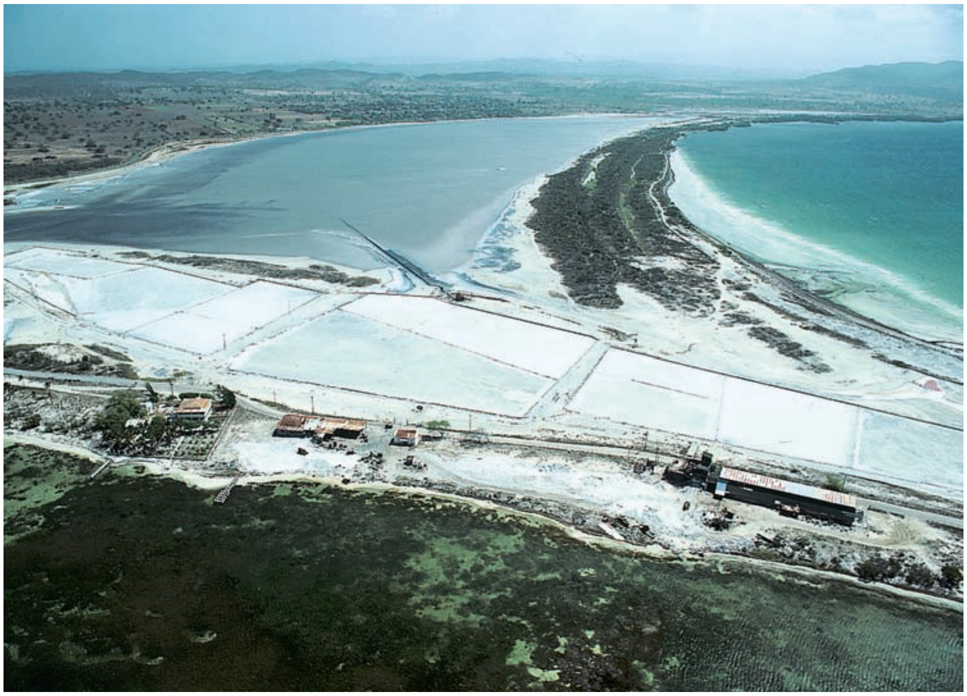


FIGURE 17.20 Aerial view of salt-evaporating ponds on the southwestern tip of Puerto Rico. The shallow ponds are flooded with seawater, and the sun and wind evaporate the water. Ponds like these have also become an important habitat for seabirds.

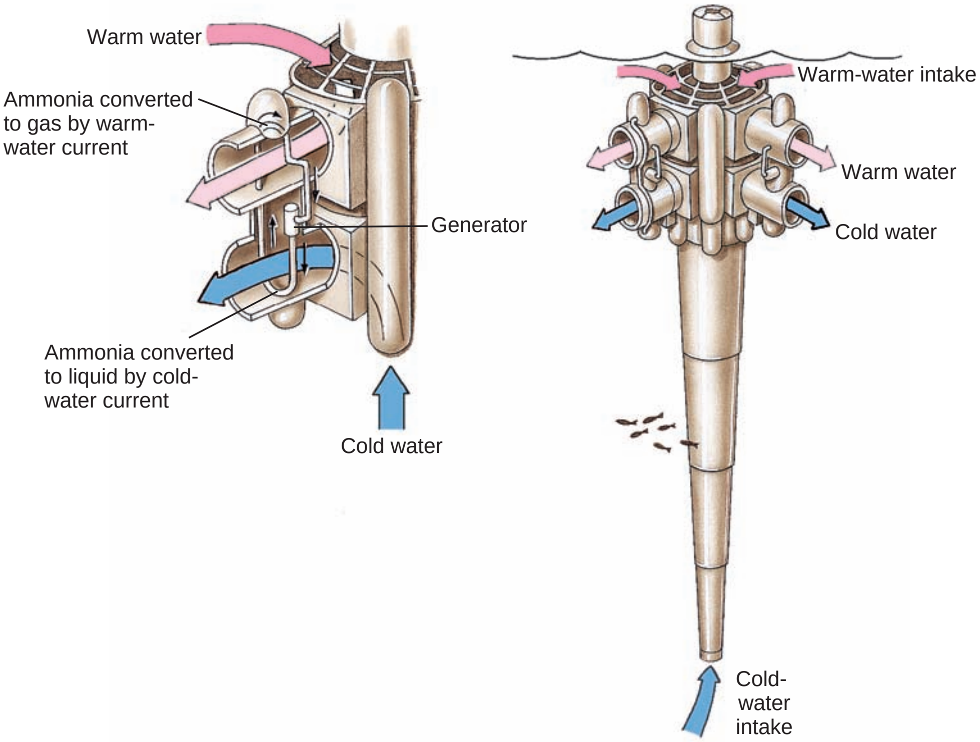

Warm water
Ammonia converted to gas by warm-water current
Generator
Ammonia converted to liquid by cold-water current
Cold water
Warm-water intake
Warm water
Cold water
Cold-water intake

FIGURE 17.21 This ocean thermal energy conversion (OTEC) plant is an experimental model consisting of a platform containing a control room, living quarters, and generators, plus a tube several hundred meters long for collecting cold water.

in northwestern France, since 1966. A few other facilities have been built on an experimental basis in western Europe, Canada, and other countries. One became operational in New York's East River in 2006.

The use of tidal energy is pollution-free and relatively efficient, but the resulting changes in the tidal patterns can be highly destructive to the nearby environment. The rich marshes in estuaries may be damaged or destroyed. Pollutants from other sources tend to accumulate upstream because normal tidal flushing is restricted. River flows can also be altered, increasing the risk of floods inland. On the other hand, the artificial lagoon created upstream can be used in recreation, as in the case of the French plant.

Wind-generated waves and strong ocean currents are other potential sources of energy, particularly in areas subject to powerful, regular waves. As with tidal energy, water flow can be converted into electricity by turbine generators. Wave energy is also used to power navigation buoys. Several projects, mostly in western Europe, plan to use waves to produce energy for seawater desalination or to pump nutrient-rich deep water to the surface for use in mariculture.

Another way to harvest energy from the ocean is to take advantage of the temperature difference between surface and deep water, a process called **ocean thermal energy conversion (OTEC).** Pilot OTEC plants (Fig. 17.21) circulate ammonia, propane, or another liquid that boils at low temperature through pipes bathed in warm surface water. The liquid evaporates and the gas is forced through turbine generators to produce electricity. The pipes then flow through cold water pumped up from the deep, condensing the gas back into a liquid, and the cycle repeats. This process, in which a difference in temperature is used to produce electricity, is like the reverse of a refrigerator, which uses electricity to produce a difference in temperature between the inside and outside. Temperature differences of at least 20°C (36°F) between the surface and below are needed, a condition met in the tropics. Electricity generated by OTEC could be sent ashore by power lines, or used at sea for various industrial operations. The cold, nutrient-rich water pumped from the deep can also be used in mariculture for human food (see Fig. 17.16) and to grow algae for animal feed and plant fertilizers.

Potential sources of electricity from the sea include tides, waves, currents, and the temperature difference between surface and deep water.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. For the last three years the annual catches of a commercially important fish have been above the maximum sustainable yield. One option is to decrease the fishing effort by decreasing the number of fishers. This, however, would cause unemployment in a region where unemployment is already high. What other options might ensure a lower fishing effort? How could they be carried out?
2. The mariculture of many food species is expensive, and often only high-priced species are raised. This type of mariculture is of little help to the poor nations where food is needed the most. What measures and new developments might help increase the value of mariculture to these poor nations?
3. It has been suggested that cheap electricity generated from tides, waves, or currents could be used to pump nutrient-rich water from the deep. The water could then be used to grow algae to feed the larvae of farmed fishes and invertebrates. How else could this energy be used to decrease the costs of mariculture?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

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18
CHAPTER

The Impact of Humans on the Marine Environment

HARBOUR AREA
POLLUTED
by RAW SEWAGE
PARA

The media offer disturbing news about the health of the oceans. Stories about global warming, pollution, dying coral reefs, and vanishing sea life are all too familiar. This is, however, only a small sample of **anthropogenic impacts,** or the effects of human activities, on the marine environment. More than 6.5 billion people now live on our planet (see Fig. 17.2), and more people now live within 100 km (60 mi) of the coast than lived on the *whole* planet in 1950! Everywhere, not just along industrial areas, the pressures of civilization are modifying the marine world. Water quality has decreased, fisheries are imperiled, recreational areas are at risk, and new health hazards are developing.

MODIFICATION AND DESTRUCTION OF HABITATS

Pollution is, unfortunately, not the only or necessarily most important way we affect the marine environment. This section briefly summarizes problems caused by human activities like dredging, the dumping of silt or mud, landfilling, or even of the use of explosives. Such activities modify or destroy **habitats,** the places where organisms live (Fig. 18.1). The effects of such physical disturbances are direct and immediate, as opposed to indirect effects like those of pollutants released somewhere else. The indirect effects of destruction of habitats, however, can be over much larger areas, as when the nursery grounds of fish are destroyed.

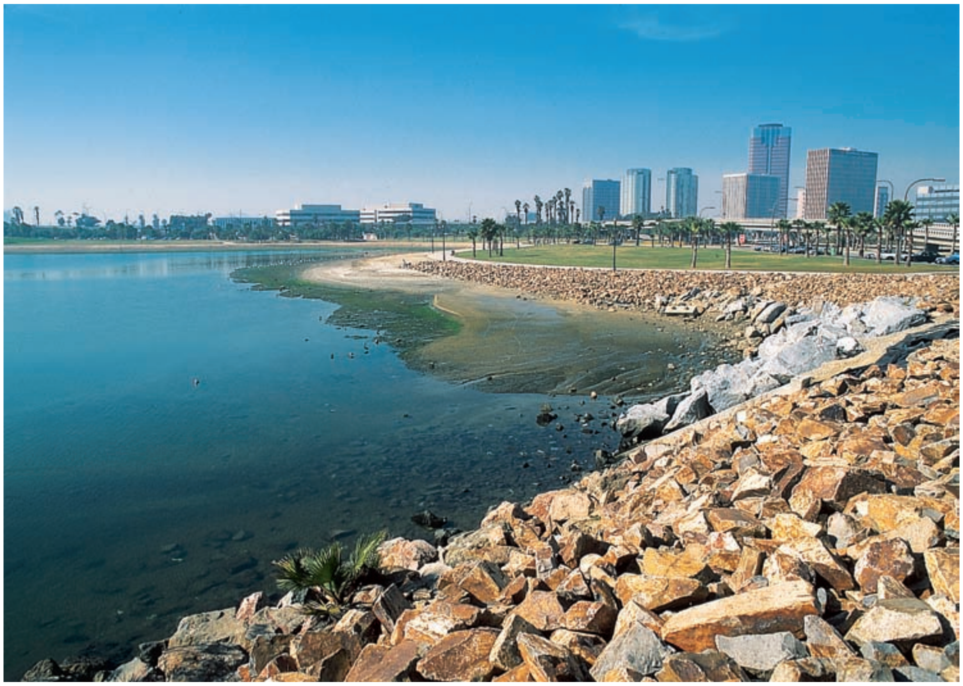


FIGURE 18.1 Salt marshes in Southern California and in many other locations around the globe have been obliterated with reclamation.

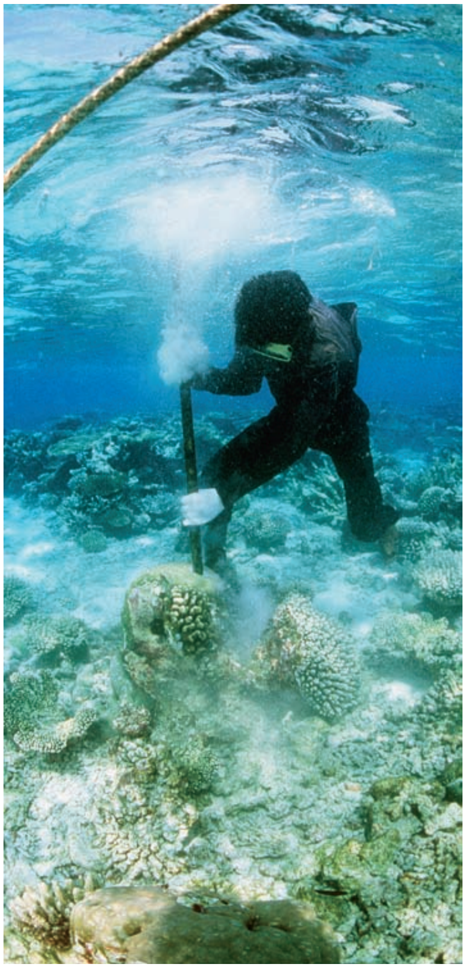


FIGURE 18.2 Coral mining in the Maldive Islands, Indian Ocean. Reef-building corals are widely used as construction material in many parts of the tropics. Coral was used in the Maldives to build part of a new airport runway, even if the islands rely on their coral reefs to attract tourists, an important sector of the economy.

Most destruction of habitats takes place along the coast close to where people live, as in estuaries and mangrove forests (see "Human Impact on Estuarine Communities," p. 281). It results mostly from unplanned or poorly planned coastal development. The problem is more acute in developing nations, where population growth, poverty, and the absence of effective management are harmfully combined. The destruction of coastal habitats is certainly not restricted to poor countries, however. Growing cities, increased tourism, and development for industrial and recreational uses have radically altered the coastlines of the richer nations as well.

Coral Reefs

Coral reefs are threatened by human activities all over the tropics. More than a quarter of the world's coral reefs have already been lost or are at high risk. Though coral reefs support luxuriant life that provides much-needed protein and potentially life-saving drugs, they are subjected to much anthropogenic stress. This includes pollution by excess **nutrients** from sewage (see "The Kāne‘ohe Bay Story," p. 310) and agricultural runoff, overgrowth by seaweeds (see "Grazing," p. 324), and overfishing. Like their also-threatened terrestrial counterparts, the tropical rain forests, coral reefs are among the oldest and richest environments on earth. Ironically, the rapid disappearance of tropical rain forests threatens coral reefs, too. The clearing, or deforestation, of the forests for agriculture, logging, and urban expansion increases the amount of soil washed out to sea by the plentiful tropical rain. In some places the resuspension of sediments by nearshore dredging also increases sediment loads.

Corals can tolerate moderate levels of sediment, but the higher levels produced by human activities may smother them. Furthermore, young corals do not settle on surfaces that are covered with sediment. Another harmful effect is that sediment in the water makes it more murky, reducing the amount of light that reaches the corals, which depend largely on food produced by **zooxanthellae.** Due to these various effects, sedimentation is a serious threat to many of the world's reefs.

Coral reefs are extensively damaged or destroyed by explosives used to kill fishes. Even though illegal, dynamite fishing is practiced in many places. It may take several decades for damaged coral reefs to recover their former splendor. Explosives also are used to open navigation channels.

Fishing with poisons such as bleach and cyanide kills corals as well. Though this is generally banned, such poisons are widely used in Southeast Asia and parts of the western Pacific. Other threats are the mining of coral for construction material (Fig. 18.2) and the indiscriminate collection of corals for the

Nutrients Raw materials other than carbon dioxide and water that are needed by *primary producers* for *primary production.*
- Chapter 4, p. 68

Zooxanthellae Dinoflagellates (single-celled, photosynthetic algae) that live within animal tissues.
- Chapter 5, p. 96; Figure 14.1

aquarium trade and for sale as souvenirs and decorations. Shell collectors can be very destructive to coral reefs by turning over or breaking corals to get their specimens. Damage by anchors, fish traps, reef walking, and scuba diving has also taken their toll.

Another indication of stress to coral reefs is the worldwide outbreaks of mass coral **bleaching.** Shallow parts of about more than half of all coral reefs around the world showed bleaching in 1998. Biologists are increasingly concerned that global warming is causing higher water temperatures and thus more frequent, widespread, and severe bleaching events. Bleaching occurs when corals expel their symbiotic zooxanthellae, causing white patches to form on the colonies (Fig. 18.3). Recovery may take place because corals have different species of zooxanthellae and a new type may replace one that has been expelled. Bleached corals never lose all their symbionts. Even dying colonies have large numbers of zooxanthellae in their tissues, not enough to give color but enough to reestablish normal numbers when conditions are better. Bleached corals, however, do not grow and are vulnerable to disintegration.

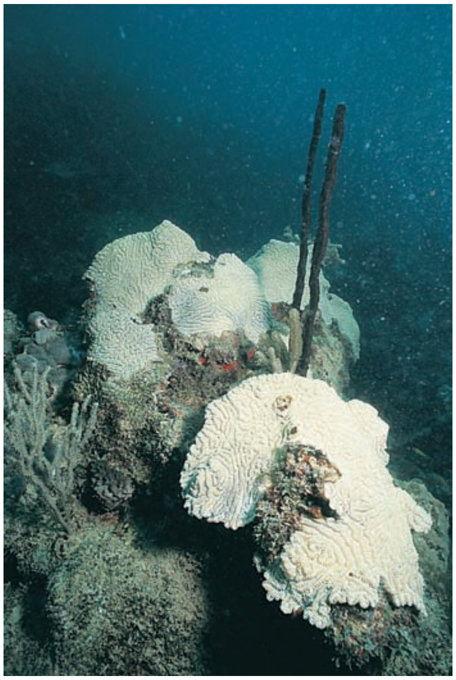


FIGURE 18.3 These colonies of a brain coral (*Meandrina meandrites*) in the Caribbean have become almost white after losing their symbiotic algae, or zooxanthellae, a phenomenon known as bleaching.

An increase in the appearance of killing diseases is additional evidence of coral stress. Infections typically show as a line of discolored dead tissue that exposes the underlying white skeleton as it advances over the colony. Various infections have been described, and their names ("black-band disease," "white-band disease") refer to the color of the advancing infection. These diseases (see Fig. 14.17) seem to be caused by bacteria and fungi that take hold on colonies damaged or stressed by excess nutrients.

Another major problem threatening corals is **ocean acidification,** which is caused by the increase in atmospheric CO_2. An increase in the acidity of the water makes the calcium carbonate ($CaCO_3$) skeleton of corals more soluble and it inhibits coral growth (see "Ocean Acidification: The Other CO_2 Problem," p. 235).

Coral reefs are being destroyed in many parts of the world as a result of direct human interference, which includes the use of explosives, indiscriminate collection, damage by anchors and divers, and potentially by ocean acidification.

Trawling

Trawls that are dragged along the bottom for fish and shrimp are a major threat to subtidal habitats. Trawling scours the seafloor and leaves scars on soft sediments, particularly muddy bottoms. It also causes the resuspension of sediment, which kills suspension feeders. On hard bottoms trawling breaks off many attached animals, some of which, like sponges and tubeworms, offer shelter to juveniles of fishes and other animals. Trawling also displaces or overturns boulders, harming or killing organisms living on their surface and exposing others to predators. Repeated trawling gives bottom communities little chance of recovery. The total number of species ultimately decreases markedly because the continuous disturbance favors short-living, fast-reproducing species like small worms, while long-living, slow-reproducing animals like sponges, clams, and sea stars tend to disappear. Deep-water trawling also threatens many vulnerable species that inhabit seamounts in deep water (see "Biodiversity in the Deep Sea," p. 375).

POLLUTION

Pollution—visible or invisible and on land, air, or water—is an unwanted but familiar part of our lives. **Pollution** can be described as the introduction by humans of substances or energy that decreases the quality of the environment. Many of these substances, or **pollutants,** are artificial substances that do not occur naturally. Some substances, however, have natural sources, such as natural oil seeps and volcanic eruptions, which are not considered to be sources of pollution. By contrast, the liberation by humans of naturally occurring substances, for example, when mining releases metals that are naturally stored in rocks, is considered to be pollution.

The role of humans in decreasing the quality of the marine environment has been enormous. The potentially detrimental effects of pollution can directly or indirectly affect all parts of the ocean, from beaches to the deepest depths. Pollution can also present a hazard to human health when marine organisms are eaten or when we go swimming, diving, or surfing.

Pollution is the introduction or release of substances or energy that decrease the quality of the marine environment. Many pollutants are toxic or harmful to marine life.

There is considerable diversity in the types, distribution, sources, and effects of marine pollutants, but most pollution comes from land-based sources, that is, from human activities on land. Major land-based pollution sources include urban development, agriculture and forestry, transport, industry, and power generation. The most important sea-based sources are shipping and offshore oil drilling, but these account for less than 20% of the total pollution that enters the ocean. Here we will briefly discuss only the most important types of marine pollutants and some of their effects on marine life.

Eutrophication

Fertilizers in agricultural runoff and sewage are major anthropogenic sources of nitrate, phosphate, and other nutrients to the marine environment. Atmospheric input from fossil fuel combustion is another major source of nitrogen, the largest, in fact, to the open ocean. Anthropogenic inputs of nitrogen to the oceans now exceed natural inputs. Thus, humans have come to dominate the global nitrogen cycle, and the situation will intensify because fertilizer use, fossil fuel combustion, and other human activities that increase nutrient inputs to the sea are ever expanding.

Though nutrients are needed by marine primary producers, excessive amounts encourage too much algal growth, a phenomenon known as **eutrophication** (see "Overwhelming the Nitrogen Cycle," p. 236). Eutrophication is primarily a problem of coastal waters, particularly in shallow, partially enclosed areas. Eutrophication can damage important habitats such as seagrass beds and coral reefs by causing a chronic increase in phytoplankton abundance, reducing the penetration of sunlight to the bottom, and accelerating the growth of seaweeds that overgrow the bottom (see "The Kāneʻohe Bay Story," p. 310). It may also trigger phytoplankton blooms, the short-term, explosive increases in the abundance of **phytoplankton.** Blooms of phytoplankton and particularly of bottom-dwelling cyanobacteria are sometimes toxic.

Organic matter in the form of the remains of the phytoplankton blooms and the feces of the zooplankton and fishes that feed on the plankton fall to the bottom, threatening already depleted fisheries. **Decay bacteria** then break down the organic matter. Bacteria may completely use up the oxygen on the bottom, causing **anoxic conditions.** Seasonal **hypoxic** (or "dead") **zones,** areas where the water lacks oxygen, that result from the effects of agricultural runoff have become common in a number of areas, including the Gulf of Mexico, (see "Gulf of Mexico's Hypoxic Zone," p. 406), Chesapeake Bay, and the Baltic Sea. About 150 hypoxic zones have been identified in oceans around the world (see "Special Report: Our Changing Planet," Fig. 14).

Coastal pollution may also be causing frequent red tides and other phytoplankton blooms (see "Red Tides and Harmful Algal Blooms," p. 334). These events seem to be occurring more frequently in many coastal waters. In Japan and China, for example, they endanger valuable mariculture operations. Blooms of phytoplankton and other algae have also become a recurrent problem in the Baltic and Adriatic seas. They cause millions of dollars worth of damage to fisheries, mariculture, and tourism.

Agricultural runoff, fossil fuel combustion, and other sources of increased nutrient inputs to the ocean are responsible for eutrophication, the excessive growth of phytoplankton and seaweeds.

Ironically, cutting down the amounts of nutrients that naturally enter the ocean can also be harmful. Dams and reservoirs that divert water for agricultural and other uses reduce the amount of nutrients that otherwise would have enriched the productivity of coastal regions, thus affecting fisheries. The building of dams and the diversion or canalization of rivers also reduce the amounts of sediments entering the ocean, severely increasing the erosion of the immediate coast.

Sewage

Disposing of ever-increasing amounts of **sewage** is a major problem in cities around the world. **Domestic sewage** carries all kinds of wastewater from homes and city buildings. It may also carry storm runoff water. **Industrial sewage** contains a variety of wastes from factories and the like. Most of society's sewage is discharged into the sea, or into rivers that flow to it. The vast amounts of sewage that enter the ocean threaten both the marine environment and human health.

Impacts of Sewage Sewage discharges into coastal waters are a serious health hazard, a threat more serious than once thought. Sewage contains many viruses, bacteria, and other parasites that cause disease. Infectious hepatitis, for example, is carried by viruses found in human feces. Some 2.5 million worldwide cases of infectious hepatitis annually result from people eating oysters, clams, and other shellfish that concentrate the viruses as they filter the water for food. Swimming in sewage-polluted water can also be hazardous; people can get sick from swallowing contaminated water or develop ear, throat, and eye infections just from contact with the water. The closing of beaches because of spills of raw sewage, common when sewers overflow after a rainstorm, has now become routine in many areas, especially where sewage and stormwater are discharged near shore. It has been recently estimated that in Southern California alone there are 1.5 million annual cases of gastrointestinal illnesses among recreational users as a result of sewage pollution, with a health cost of over $400 million. The economic impact due to lost tourism and the closure of shellfish farms can be considerable.

Sewage is discharged into the sea by many communities around the world. Sewage is a major health hazard to humans because it spreads disease.

Sewage Treatment and Sludge The harmful effects of sewage can be reduced by **sewage treatment,** and many countries require by law some form of treatment before sewage is discharged. The sewage may simply be allowed to sit in a basin for a time, so that much of the solid matter settles out. A more advanced, but also more expensive, option is to allow decay bacteria and other organisms

Phytoplankton The minute, drifting organisms that are a critical part of open-water communities because they perform practically all the photosynthesis in the open ocean.
- Chapter 15, p. 330

Decay Bacteria Bacteria and archaea that break down, or decompose, non-living organic matter into nutrients and other simple chemicals.
- Chapter 5, p. 87

Anoxic Conditions Absence of oxygen that results in the accumulation of *hydrogen sulfide* (H_2S) in the sediment, which turns the sediment black.
- Chapter 11, p. 260

EYE ON SCIENCE

Gulf of Mexico's Hypoxic Zone

The Gulf of Mexico is North America's most economically productive body of water, in part because of its rich commercial and recreational fisheries. Four of the top five U.S. fishery ports are in the Gulf of Mexico, and the Gulf generates about 20% of the total fisheries landings of the nation. The northern portion of the Gulf contains almost half of the nation's wetlands, and these wetlands, plus the region's seagrass beds, are essential habitats for the young of commercially important shrimps and fishes.

Threatening life in this northern section is the seasonal Gulf of Mexico's hypoxic zone (see "Overwhelming the Nitrogen Cycle," p. 236). The total area of the Gulf's hypoxic zone averaged 8,252 km^2 (3,186 mi^2) from 1985 to 1992, almost doubling to an average of 15,632 km^2 (6,036 mi^2) from 2000 to 2005 (see "Special Report: Our Changing Planet," Fig. 15). It is one of the largest hypoxic, or "dead," zones in the Northern Hemisphere.

Current research projects by the Center for Sponsored Coastal Ocean Research (CSCOR) are investigating the causes and the effects of hypoxia in the northern Gulf of Mexico. Being studied are the chemical, physical, and biological factors that influence the development of hypoxia, paying particular attention to the continental shelf off Louisiana. The main culprit of hypoxia in the Gulf is eutrophication caused by the huge amount of nutrients, especially nitrates, brought in by the Mississippi River. CSCOR research has shown that the source of most of the excess nutrients is fertilizers from agricultural runoff (see "Eutrophication," p. 405).

In addition to marine biologists, the investigation involves chemical and physical oceanographers. Factors such as nutrient inflow, circulation patterns, and freshwater input are being monitored. Research on the effects of hypoxia on the distribution, reproduction, and general health of commercially important shrimps and fishes is also being undertaken. It has been hypothesized that hypoxia may indirectly cause declines in the availability of food, increases in the exposure to predators, habitat loss, and even changes in behavior, particularly schooling among fishes. One project is looking at pelagic food webs by examining the distribution and abundance of open-water organisms from bacteria to fishes. Of special concern are changes in the distribution and mortality of endangered species such as sea turtles and cetaceans.

CSCOR projects aim to ultimately predict the extent and impact of hypoxia, particularly on fisheries. This will hopefully permit the implementation of strategies to change eutrophication and hypoxia conditions. A mathematical model has already suggested that a 30% reduction in the concentration of nitrogen entering the northern portion of the Gulf by 2015 may reduce the average size of the hypoxic zone to less than 5,000 km^2 (1,930 mi^2).

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

to break down the organic matter in the sewage. The addition of chemicals or other steps may be included to further purify the sewage. After treatment, the sewage is often disinfected by using chlorine to kill bacteria and some of the viruses. Ozone treatment and UV irradiation are other methods of disinfection. Sewage that contains industrial waste may also contain pesticides, heavy metals, and other toxic chemicals. Advanced forms of treatment can nevertheless produce water that is pure enough to be used for irrigation or even drinking water.

Sewage treatment greatly reduces the impacts of sewage on the marine environment and human health, but it is not without drawbacks. The cost of sewage treatment increases sharply as more advanced treatment methods are used, and many communities cannot afford it. Chlorine used for disinfection may remain in the discharged wastewater and is toxic to marine life. Sewage treatment also creates a new waste disposal problem: what to do with **sludge,** the wastes that are taken out of the sewage. This semiliquid material is much more concentrated than the original sewage and often contains high levels of heavy metals and other toxic substances. If the sludge is disposed of in the ocean, it smothers the natural communities on the bottom, creating black deserts around outfalls (Fig. 18.4).

It is impossible for most detritus feeders to handle the massive amounts of organic matter contained in sludge. The organic matter is instead decomposed by bacteria that thrive under these conditions. The decay bacteria use oxygen to such an extent that anoxic conditions develop. The total number of species decreases as many of the natural inhabitants disappear. They are replaced by hardier forms of life, such as certain species of polychaete worms. Bottom fishes collected around sludge disposal sites tend to show skin tumors, erosion of fins, and other abnormalities, apparently a result of the high concentration of toxic substances, viruses, and bacteria.

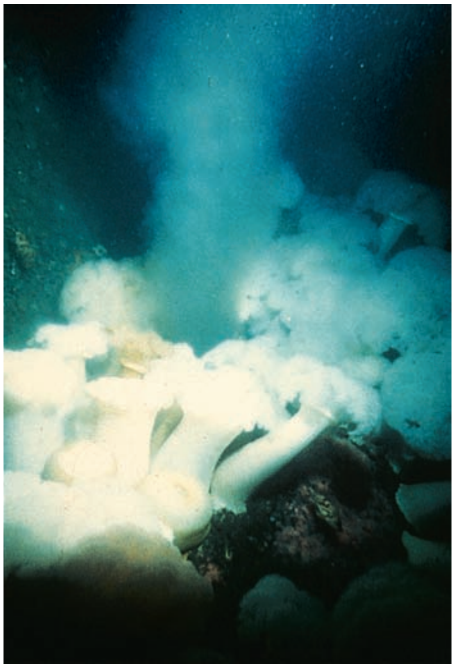


FIGURE 18.4 Treated sewage effluents from the Hyperion treatment plant being released at a depth of 60 m (180 ft) at the end of an 8-km (5-mi) outfall in Santa Monica Bay, Southern California. Large sea anemones (*Metridium*) surround the site. Santa Monica Bay is actually getting cleaner. The disposal of sludge from another treatment plant ended in 1987, and part of the wastewater at this outfall is now undergoing additional treatment. Treatment at the plant has been improved in order to meet standards set by the Environmental Protection Agency.

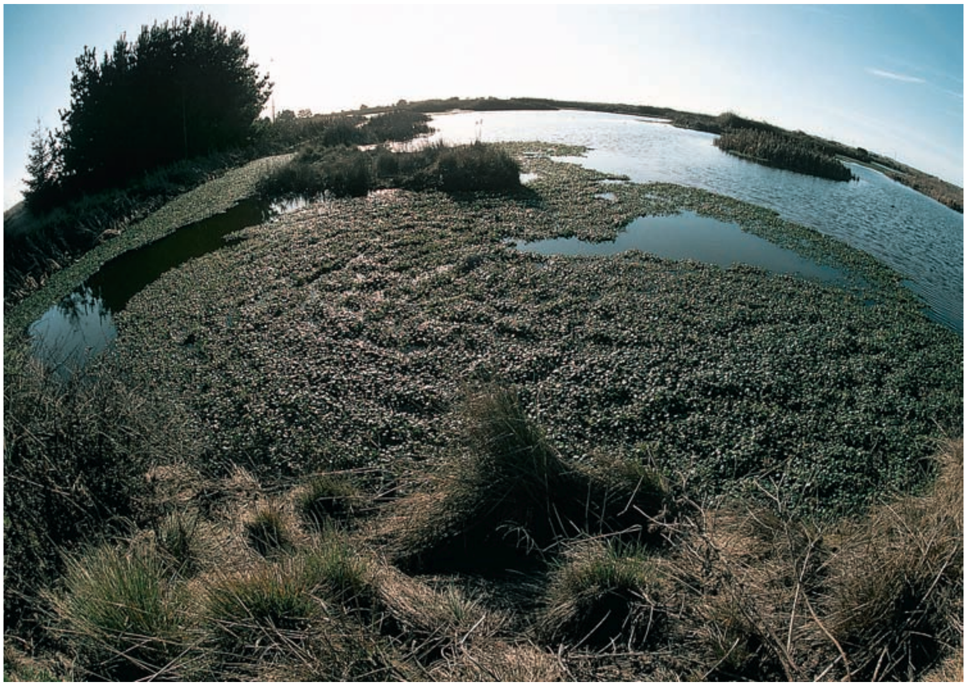


FIGURE 18.5 This lush artificial marsh is part of a network of marshes where domestic sewage from the town of Arcata in northern California is naturally purified before it is piped into the ocean. Sewage, which is mostly water, is given preliminary treatment, and chlorine is added to kill harmful bacteria. It is then pumped into the marshes, where mud bacteria break down the organic matter. The released nutrients fertilize the marsh plants. The marshes prevent the pollution of the ocean by sewage and attract many species of birds and other wildlife.

It is possible to implement alternatives to the discharge of sewage into the sea. Some communities take advantage of the ability of marshes to recycle nutrients by using the marshes for natural sewage treatment (Fig. 18.5). Additional and improved treatment, mandated in the United States by the Clean Water Act of 1972, has reduced the amount of suspended solids in the sewage being discharged in the country. But why not consider sewage a resource and turn it into something useful? Ideally we could recycle the large amounts of precious water and nutrients that go to waste. Sludge is sometimes recycled into landfill, construction blocks, and compost. It is also spread on farmlands as fertilizer, burned to generate electricity, and converted into fuel.

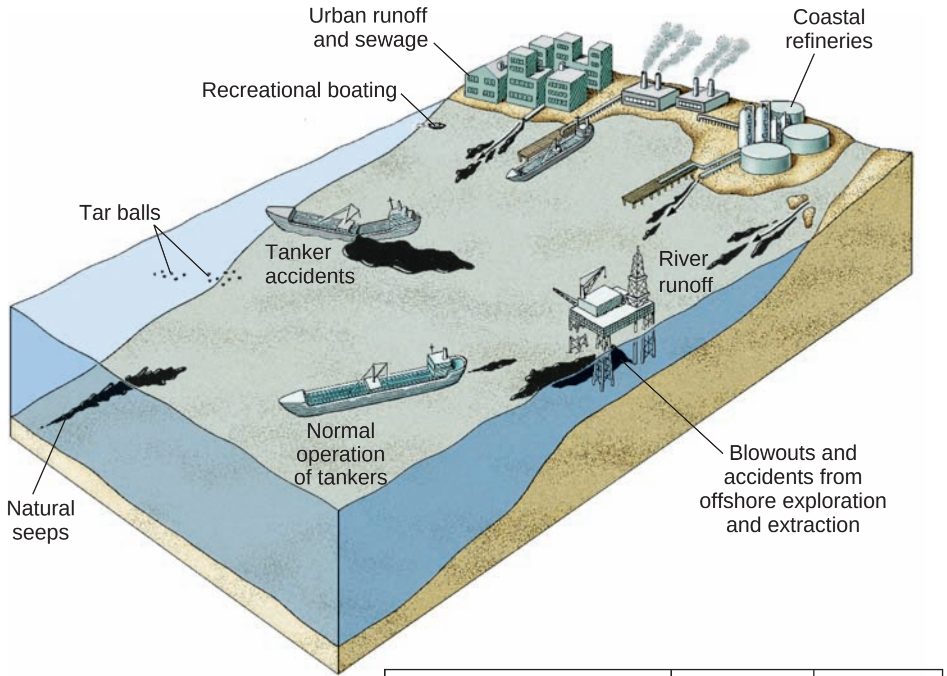
High volumes of sludge discharged into the sea greatly modify or destroy bottom communities.

Oil

Crude oil, or **petroleum,** is a complex mixture of **hydrocarbons,** long chains of carbon and hydrogen, and certain other chemicals. Crude oil is refined to yield not only fuels but raw materials for making plastics, synthetic fibers, rubber, fertilizers, and countless other products.

Sources Oil is one of the most widespread pollutants in the ocean. An estimated 682 million tons of oil and derivatives like fuel and lubricating oil enter the world oceans each year as a result of pollution. Oil from natural seepage, not a pollutant, contributes another 584 million tons worldwide. Natural seeps are the most important source of oil in North American waters, however, around 160,000 tons a year, while different sources of pollution contribute more than 96,000 tons annually (Fig. 18.6). Almost 85% of the polluting oil in North America comes from river runoff, coastal cities, fuel from small boats and jet skis, and fuel jettisoned by planes. The remaining 15% comes from tanker and pipeline spills and as a result of exploration and extraction from the seabed.

One metric ton of crude oil = 7.33 barrels (bbl), or 308 U.S. gal.



Sources of Oil Pollution in North America	Estimated Amount	Percentage
Natural seeps	160,000 tons	60%
Land-based pollution and recreational boating	84,000 tons	28%
Transportation of oil	9,100 tons	9%
Exploration and extraction	3,000 tons	3%

FIGURE 18.6 Annual sources of oil in the marine environment.

The massive oil spills that result from the sinking or collision of supertankers, however, are the most devastating to the marine environment. The 1978 grounding of a supertanker, the *Amoco Cadiz,* poured 230,000 tons of crude oil along the coasts of northwestern France. In 1989 more than 35,000 tons of crude oil were spilled by the *Exxon Valdez* along the coast of southern Alaska, the home of whales, sea otters, salmon, bald eagles, and other wildlife. Accidents have prompted tighter restrictions, such as having double hulls, on the construction and operation of tankers. Older tankers, however, do not necessarily have double hulls. Many still navigate busy shipping lines.

Most of the components of oil are insoluble in water and float on the surface. They appear as thin, iridescent slicks on the surface or as black deposits on the shore. You would expect large areas of the ocean to be covered with the oil that has accumulated over the years. Fortunately, some of its lighter components evaporate. Oil is ultimately broken down, or decomposed, by bacteria and thus is almost completely **biodegradable.** The breakdown rate is usually slow but varies among marine communities.

Some of the components of crude oil sink and accumulate in sediments, especially after the lighter ones evaporate. Other residues remain on the water surface and form tar balls, which are common along shipping lanes worldwide. They may persist for many years in the water and have been observed in remote areas far from shipping traffic. Some even have barnacles living on them! Extensive oil spills form huge layers that coat everything in their path as they are carried by wind and currents.

The oil and shipping industries have nevertheless made considerable progress in the protection of the marine environment. Illegal dumping is still a problem but it is becoming less severe. An indication of this is a decrease in the number of tar balls on many beaches.

Oil is a widespread pollutant that enters the sea as waste from land, from accidents during its extraction from the seabed, and as a result of its transportation across water.

Effects of Oil on Marine Life Even in small amounts, oil has a variety of effects in marine organisms. Organisms may accumulate oil components, many of which are toxic, from the water, sediments, and their food. There is evidence, for instance, that compounds found in oil interfere with the reproduction, development, growth, and behavior of many organisms. These compounds are released from oil for many decades. Oil also increases susceptibility to diseases in fishes and inhibits the growth of phytoplankton. Crude oils vary markedly in their chemical composition, and therefore in their toxicity and environmental persistence. Refined products such as fuel oils tend to be more toxic than crude oil.

Major oil spills can have disastrous effects in coastal environments. Seabirds and marine mammals like the sea otter are particularly susceptible. Many die of exposure when their feathers or hair is coated with oil (Fig. 18.7), which affects their ability to maintain the thin layer of warm air needed for insulation. Birds that rely on flying to catch food are unable to do so and die of starvation. It is difficult to determine the number of birds killed by oil spills because many sink without reaching the coast, where the corpses can be counted. About 3,200 dead birds, some belonging to rare species, were counted immediately after the *Amoco Cadiz* spill. The *Exxon Valdez* spill is believed to have killed between 100,000 and 300,000 seabirds and 3,500 to 5,000 sea otters. Estimates are that it will take up to 70 years for the wildlife in the area of the spill to recover fully. Sea otters and other wildlife are still affected by low fertility and high death rates.

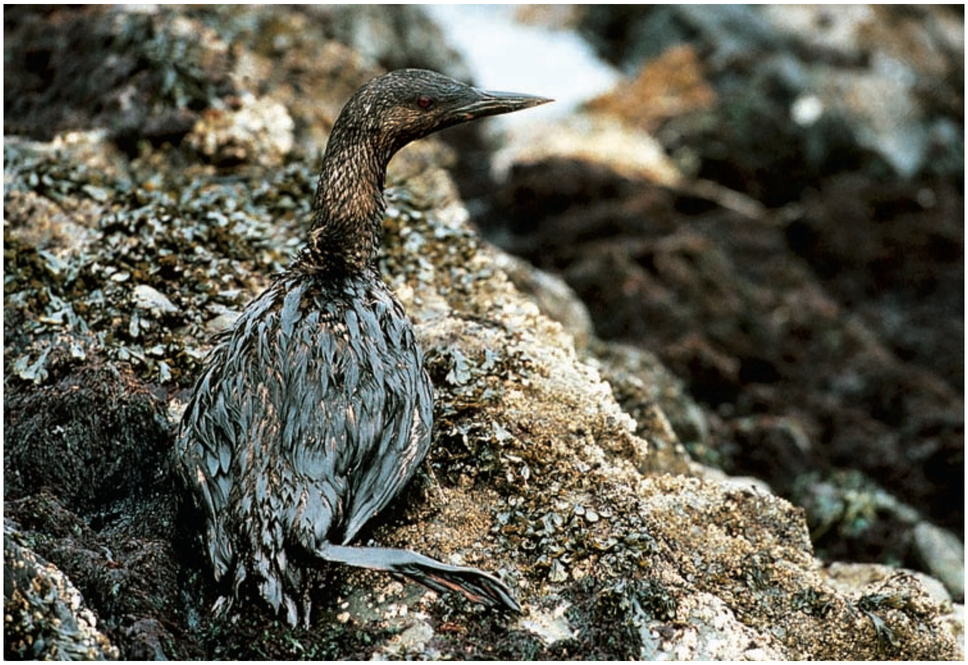


FIGURE 18.7 An oil-coated loon (*Gavia*) during the *Exxon Valdez* spill in Alaska. Detergents, which can be used to disperse the oil and help prevent situations like this, were widely used during the *Torrey Canyon* spill on the English coast in 1967 but proved to be toxic and actually caused more damage than the oil itself.

The effect of oil spills on exposed rocky shores is less devastating than it may appear at first sight. Initially there is mortality among many attached inhabitants, but wave action and tides help clean away the oil. Rocky shore communities do recover, though recovery is dependent on factors such as the amount of oil, wave action, and temperature. Degradation by bacteria takes place, but usually slowly, especially in cold water. Spills may be degraded more quickly by bacteria if an oil-soluble fertilizer is added to the water or sprayed on rocks and sediment. Experience has shown that recovery begins within months and that an apparently near-normal condition may occur as early as one or two years after the spill. Higher oil concentrations in sediments and isolated pockets, however, have been found to remain for 15 years or longer.

Large spills can have more catastrophic effects when they drift to salt marshes and mangrove forests. These communities are characteristic of sheltered coasts and estuaries where oil cannot be dispersed by wave action. Massive mortality of the dominant plants takes place, and recovery is very slow. Oil is absorbed by the fine sediment characteristic of these communities and may persist for more than 30 years in salt marshes. Coral reefs and seagrass beds also are greatly affected by oil spills. Coral colonies show swollen tissues, excessive production of mucus, and areas without tissue. Reproduction and feeding in surviving coral polyps are affected by oil. There is little evidence, however, of dramatic, long-term effects.

Oil is harmful to most marine organisms. It is especially destructive to communities typical of shallow, sheltered waters.

Containing an oil spill and cleaning up the mess is a major headache. Fencing off the spill with floating, fire-resistant booms can prevent the spill from moving into shore. "Skimmers," boats equipped with U-shaped booms, are used to skim off and recover some of the oil. These methods, however, cannot be used in heavy seas. Chemical **dispersants** are added to the spill to break the surface oil into small droplets that can then disperse in the water. Unfortunately, dispersants also are harmful to marine life, and the dispersed oil still remains toxic underwater. The use of powerful streams of hot water to wash oil from beaches after the *Exxon Valdez* spill was also harmful to many forms of life, perhaps as harmful as the oil itself.

A more recent oil spill was that of the *Prestige,* a tanker that split in two and sank off the northwestern coast of Spain in 2002. It spilled 63,000 tons of oil, creating a slick 30 km (18 mi) long that reached the Spanish coast, devastating valuable shellfish fisheries and leaving more than 100,000 people without jobs. The spill caused a general outcry that ultimately affected national elections in Spain. The *Prestige* sank with an additional estimated 40,000 tons of oil, thus creating the uncertainty of future spills.

The cost of oil spills to local economies can be enormous. Fish and filter-feeding shellfish like oysters and clams that are tainted with oil are unmarketable. The size of fish catches, particularly of bottom-dwelling species, may decrease because of the initial mortality of adults and juveniles or a drop in the abundance of their food. Furthermore, oil-soaked beaches are disastrous to resort areas dependent on tourism. Claims by those affected plus the cleanup bill can run well past the billion-dollar mark. Exxon was ordered to pay a total of $5 billion in fines for damage caused by the *Exxon Valdez.* The fine was halved to $2.5 billion in 2006, but Exxon appealed.

Persistent Toxic Substances

Many important pollutants that reach the sea from land are substances that are said to be **persistent** because they remain in the environment for years, even many decades. Persistent substances are not readily broken down either by decay microorganisms (and for this reason the substances are known as **non-biodegradable**) or by physical or chemical means in the environment.

Pesticides One group of synthetic chemical pollutants is the **chlorinated hydrocarbons.** They include many **pesticides,** chemicals used to kill insects and to control weeds, including DDT, dieldrin, heptachlor, and chlordane. Millions of tons of these and many other chlorinated hydrocarbons have been used since the 1940s, when DDT made its debut. These pesticides have been used to protect plant crops from insect pests and to control insects that carry diseases. Pesticides have saved millions of people from disease and starvation, but the unchecked use of chlorinated hydrocarbons has exposed their sinister side, the fact that they are harmful to many non-targeted forms of life.

These pesticides have not been used directly in the ocean. They are, however, carried into the ocean by rivers, runoff, and sewage and are transported long distances, even to the open ocean, in the atmosphere (Fig. 18.8). In the ocean they are absorbed by phytoplankton and particles suspended in the water and thus find their way into the food chain.

Chlorinated hydrocarbon pesticides dissolve in fats and are not excreted, so organisms tend to retain them almost indefinitely. Animals absorb and accumulate the pesticides in the organisms they eat, so their internal concentration of chlorinated hydrocarbons is higher than in their food supply. At each level of the **food chain,** then, the chlorinated hydrocarbons are more concentrated. This phenomenon is known as **biological magnification.** Among marine animals, pesticide concentrations are higher in carnivorous fishes, and even more so in the fish-eating birds and mammals at the top of the **trophic pyramid** (Fig. 18.8).

Chlorinated hydrocarbons, which include many widely used pesticides, are non-biodegradable and persistent. Many accumulate in the food chain through biological magnification.

The alarming effects of worldwide use of chlorinated hydrocarbons began to be noticed during the 1960s. Fishes caught for human consumption in the United States had to be destroyed because they contained too much pesticide. Pesticides began to accumulate in top carnivores in concentrations that were thousands and even millions of times above those found in seawater.

The effects on birds, on land and at sea, were particularly dramatic. The birds were not actually poisoned, but the high

Food Chain The steps of transfer of energy from *producers,* the algae and plants, through *consumers,* the animals.
- Chapter 10, p. 221; Figure 10.13

Trophic Pyramid The pyramid-like relationship of energy, number of individuals, or biomass of the organisms found in a food chain.
- Chapter 10, p. 223; Figure 10.16

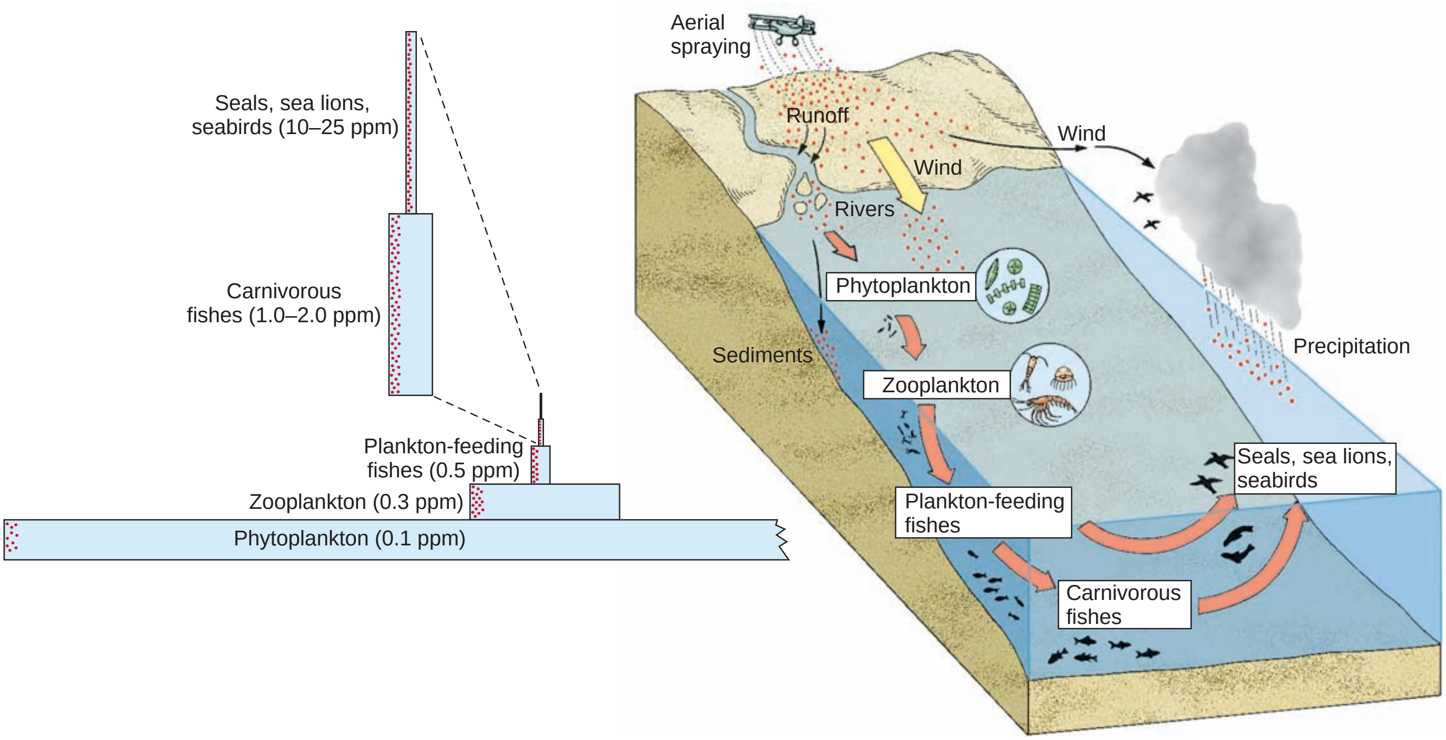


FIGURE 18.8 The concentration of chlorinated hydrocarbons increases with the relative position organisms have in the food chain, thus showing biological magnification. In the trophic pyramid that summarizes this generalized food chain, the concentration of pesticides is expressed in ppm, or parts per million.

concentrations of chlorinated hydrocarbons in their body fat interfered with reproduction, specifically with the deposition of calcium in their eggshells. The eggshells became so thin that they broke during incubation before chicks became fully developed.

The once-abundant brown pelican (Fig. 18.9), for example, became a rare sight in most of the United States due to widespread reproductive failure during the late 1960s and early 1970s. Female pelicans sat on broken eggs, or adults simply did not attempt to nest. The Channel Islands off Southern California, the last remaining nesting colony on the Pacific coast north of Mexico, recorded only one chick in 1970 and seven in 1971. High amounts of DDT and related chemicals were found in the tissues of birds taken from these and other nesting colonies and in other marine animals in the area, from filter feeders like sand, or mole, crabs to top carnivores like sea lions.

FIGURE 18.9 The brown pelican (*Pelecanus occidentalis*) is again a common sight along the coasts of the United States.

By 1972 most uses of DDT and several other chlorinated hydrocarbons were banned in the United States and many other industrialized nations. DDT residues in marine animals and sediments then began to decrease. The brown pelican, once nearly extinct in the United States, has recovered, and its reproduction has returned to normal. DDT and related residues, however, can still be found in bottom-dwelling fishes. One of these residues, DDE, was found to be degraded by bacteria under laboratory conditions. A 2000 international agreement restricting the production and use of certain toxic substances nevertheless allowed continued use of DDT because it provides inexpensive control of insects in developing nations, primarily to control the mosquitos that transmit malaria.

PCBs and Other Toxic Organic Chemicals Another problematic group of toxic chlorinated hydrocarbons are the **PCBs,** the **polychlorinated biphenyls.** PCBs are non-biodegradable and persistent and show biological magnification. They were widely used in electrical transformers and capacitors, in the manufacturing of plastics and paints, and in many other products. PCBs proved to be highly toxic, causing cancer and birth defects, and their production and use were gradually regulated or banned by many nations, including the United States in 1979.

This ban, however, came after PCBs had spread throughout the oceans. PCBs and other chlorinated hydrocarbons have been detected in the blubber of whales and other marine mammals. Salmon migrating

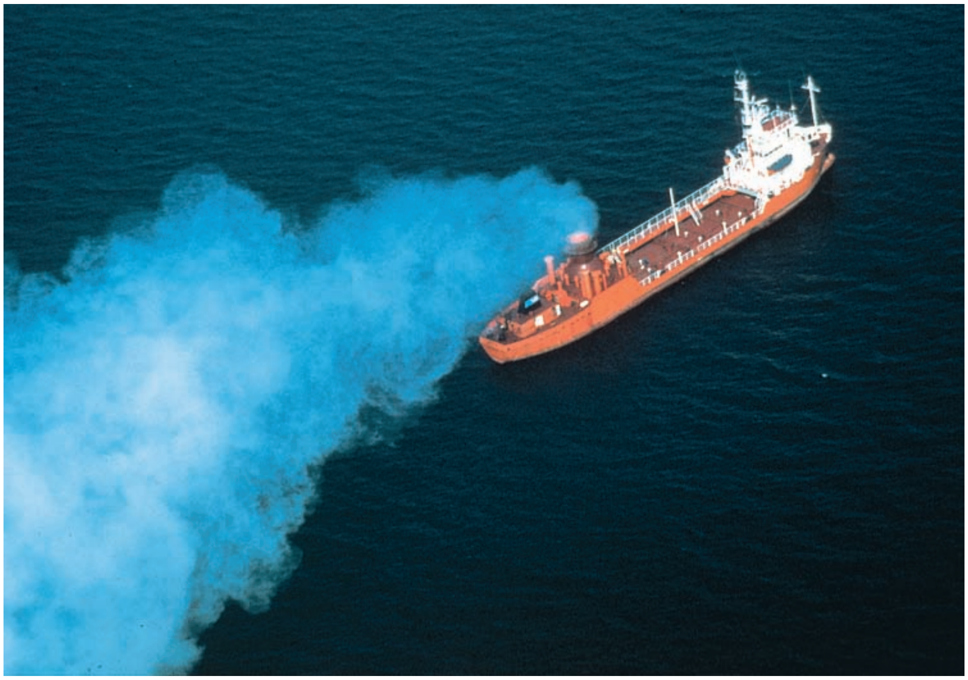


FIGURE 18.10 Hazardous chemicals such as PCBs and pesticides and other cancer-causing agents like vinyl chloride and chlorinated dioxins can be disposed of by incinerating them on the high seas rather than using dumps on land. Incinerator ships like this one burn hazardous organic chemicals at high temperatures, which results for the most part in chemicals like carbon dioxide and water. Transporting the toxic waste by sea, however, adds to the danger of spills. There are also concerns about the toxicity of hydrogen chloride and other chemicals that can be formed in the process. Very few nations dispose of all of the hazardous waste they produce on their own turf. Most simply export the waste and have other, usually poorer, nations get rid of it for a fee. A 1989 international treaty restricts, but does not ban, the international movement of toxic wastes.

to lakes and rivers release PCBs contained in their tissues when they die by the thousands after spawning. Furthermore, PCBs continue to be used in some parts of the world, and electrical equipment containing them is still around us. Such equipment is required to remain sealed and the PCBs carefully disposed of when it wears out. Invariably, though, PCBs are present in large amounts of hazardous wastes that accumulate and have to be disposed of somehow, somewhere (Fig. 18.10). PCBs are widespread in landfills and waste dumps. Like other chlorinated hydrocarbons, decades of use and disposal have also left significant amounts of these persistent pollutants in the marine environment, especially around sewage outfalls and in the sediment of harbors of industrial cities. Some marine bacteria, however, are known to degrade PCBs in sediments. They have been found mostly in areas with high concentrations of PCBs such as the Hudson River estuary.

Chlorinated **dioxins** and **furans,** two other groups of chlorinated hydrocarbons, also enter the marine environment from land. Pulp mills and waste incinerators are important sources of the chemicals, which also occur naturally, for example, as a result of forest fires. Some dioxins are among the most toxic of all chemical pollutants. They are carcinogenic and cause birth defects and damage to the immune system in many vertebrates and humans. Furthermore, they show biological magnification.

PCBs, a group of chemicals used as fire retardants (PBDEs), certain pesticides, and other toxic chemicals evaporate into the atmosphere, where the wind can carry them considerable distances before they condense in the cool upper atmosphere. When they condense, they are carried in rain or snow back to the ground, where the process starts all over again. Because of wind patterns and the fact that more condensation of the chemicals takes place near the poles, where it is cold, the chemicals are concentrated in polar regions. This global system of evaporation and condensation of substances, many of which are toxic, is known as **global distillation.** Global distillation has been implicated in whale kills, and high levels of PCBs and other toxic chemicals have been found in seals, polar bears, whales, and even the Inuit and other aboriginal peoples of the once pristine Arctic region and thousands of miles from where the pollutants were used.

PCBs, dioxins, and furans are pollutants notable for their toxicity. They are persistent and show biological magnification.

Even at low concentrations years after being banned, PCBs and other chlorinated hydrocarbons have been implicated in abnormal sexual behavior and reproductive ability in seabirds, marine mammals, and fishes. These pollutants form chemicals that are similar to sex hormones and seem to disrupt reproduction.

Heavy Metals An additional category of chemical contaminants of the world's oceans is metals, particularly those classified as **heavy metals.** Very minute amounts of some metals are needed by most if not all organisms, but an excess can be toxic.

One particularly troublesome heavy metal is **mercury,** which reaches the ocean through several natural processes: the weathering of rocks, volcanic activity, rivers, and dust particles from the atmosphere. Even so, human activities play an increasingly important role, especially along the coast. Mercury was once an active ingredient in chemicals used to kill bacteria and molds and in antifouling paints. It also is used in the production of chlorine and plastics and other chemical processes and in batteries, fluorescent lamps, drugs, and even tooth fillings. Discharges from industries and cities and the burning of coal, which contains traces of mercury, have increased the concentration of mercury in the marine environment.

Pure, liquid mercury, like that in thermometers, is harmless unless its vapors are inhaled. It is a different story when mercury combines with organic chemicals, as when transformed by some bacteria and other microbes in the water or sediment. These organic compounds, such as **methyl mercury,** are persistent and accumulate in the food chain. Levels of mercury too high for human consumption have been found in large fishes such as tuna and swordfish. The older the fish, the higher the mercury content. Methyl mercury also can be found in coastal sediments, particularly around areas where wastes are dumped. Mercury compounds also undergo global distillation. They are very difficult to eliminate and are highly toxic to practically all forms of life. In humans they can cause brain, kidney, and liver damage and birth defects.

The dangers of the presence of mercury in seafood were demonstrated by the appearance in the 1950s and 1960s of a crippling neurological disorder among the inhabitants of a town in southern Japan (Fig. 18.11). The victims were poisoned by eating fish and shellfish that contained concentrated mercury discharged at sea by a chemical plant. More recently, high levels of mercury in fish prompted the United States government in 2004 to warn pregnant women and young children to limit their intake of canned tuna, swordfish, and other fishes.

Lead is another widespread heavy metal pollutant. As with mercury, organic lead compounds are persistent and concentrate in the tissues of organisms. Lead is toxic to humans, causing nervous disorders and death. The principal source of lead pollution in the marine environment is the exhaust of vehicles run with leaded fuels. The lead reaches the water by way of rain and windblown dust. Lead has also found its way into all sorts of products, such as paints and ceramics, that eventually make their way to the ocean.

The removal of lead from gasoline has been responsible for a decrease in lead levels in surface water, especially in the North Atlantic. This represents a success story that demonstrates that environmental problems can be addressed.

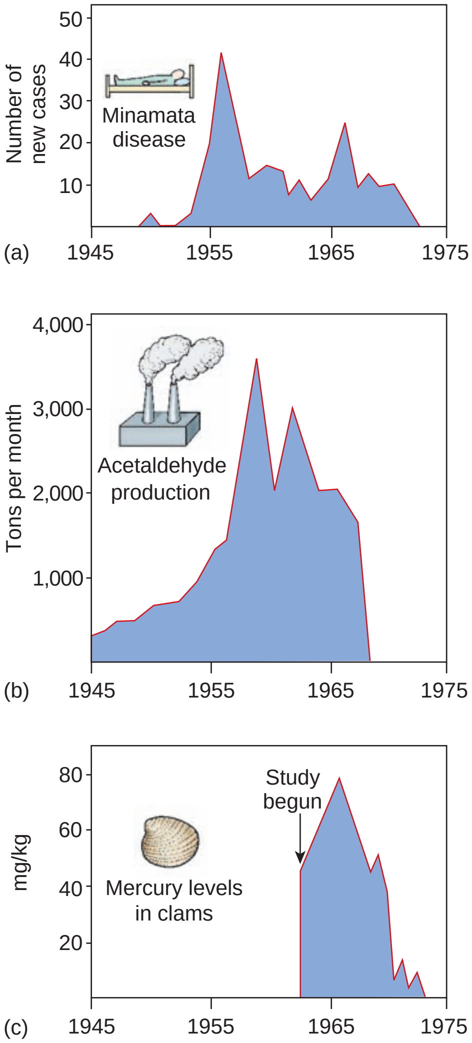


FIGURE 18.11 In the 1950s and 1960s a neurological disorder that often ends in severe brain damage, paralysis, or death appeared among the inhabitants of Minamata, Japan. The number of new cases (*a*) was directly related to the production of acetaldehyde by a chemical plant (*b*). A mercury compound was used in the production of acetaldehyde and vinyl chloride, which are used in making plastics. As a result, an estimated 200 to 600 tons of waste mercury were discharged into Minamata Bay between 1952 and 1968, when it was finally stopped. The disease, now called Minamata disease, was caused by eating seafood contaminated with mercury, here indicated by its concentration in the edible clam *Venus* (*c*).

Mercury and lead compounds are highly toxic. They are persistent and accumulate in the food chain.

Cadmium and **copper** are other toxic heavy metals that are slowly concentrated in marine life. Mining and refining operations are major sources. Cadmium is also present in the waste from battery manufacturing and in discarded batteries. Together with lead, mercury, and other toxic metals, cadmium is common in discarded computers and other electronic components. These toxic metals often seep into rivers or the ocean from disposal sites. Sources of copper include wood treatment and other industrial processes. Unlike lead and mercury, which are transported in the atmosphere, unnaturally high levels of cadmium, copper, and most other heavy metals remain localized near their source.

Radioactive Wastes Radioactive substances have been contaminating the marine world since the first atomic bomb explosions in the early 1940s. **Radioactivity** is a property exhibited by certain atoms that emit **radiation** in the form of energy or particular types of particles. Exposure to some types of radiation is harmful to all forms of life. In humans it causes leukemia and other cancers, as well as other disorders. Radioactive waste does not need to be ingested to have effects because it can penetrate through living matter. Radioactive material also may continue to emit radiation for thousands of years. Some radioactive **isotopes** occur in nature but in minute amounts, and some harmful radiation reaches us from outer space. A source of radioactivity is a by-product, or waste, of the use of the atom as a source of energy.

Radioactive waste is dangerous and must be disposed of somewhere. Some is stored in containers and dumped into designated areas of the ocean. Sunken nuclear-powered submarines and ships, fallen satellites, and crashed planes carrying nuclear weapons are other potential sources of radioactive waste. Accidents in nuclear reactors along the coast and industrial effluents add to the risk. Nevertheless, the use of radioactive material is highly regulated, so it generally poses no major threat to the marine environment.

Solid Waste

A look at the upper reaches of many beaches will reveal an amazing assortment of trash brought in by high water. Most of it is plastic: bottles, bags, foam cups and packaging, nets, and thousands of other items. Add rubber, glass, and metal and you have quite a heap of trash. Solid waste from land still flows to sea at an alarming rate, even if dumping of solid waste and other pollutants is banned by the London Convention of 1972.

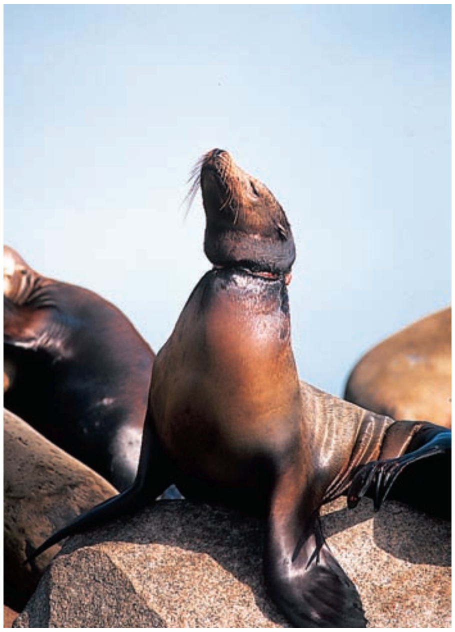


FIGURE 18.12 It has been estimated that plastic debris kills as many as 2 million seabirds and 100,000 marine mammals every year. Plastic bags kill sea turtles that swallow them, thinking they have caught a jellyfish. Six-pack rings easily ensnare seabirds, which, unable to feed or fly, face a slow death. This California sea lion (*Zalophus californianus*) is being slowly strangled by nylon fishing line.

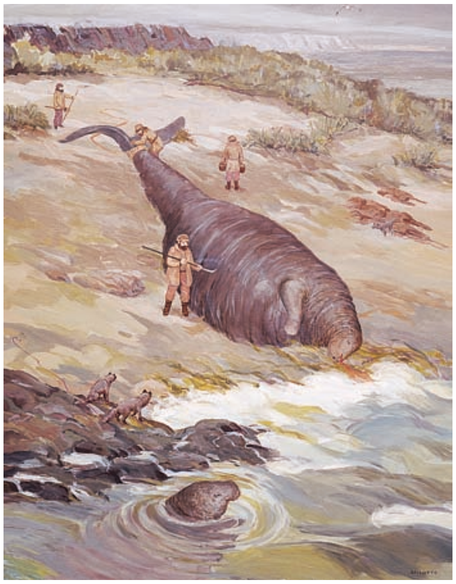


FIGURE 18.13 The Steller's sea cow (*Hydrodamalis gigas*), weighing an estimated 10 tons or more, ate mostly kelp. It became known to science in 1741, when it inhabited the kelp beds of the Commander Islands in the western Bering Sea. Demand for its meat, which was considered "as good as the best cuts of beef," led to its extermination at the hands of whalers. The species was slaughtered to extinction soon after its discovery; the last known live individual was taken in 1768.

Plastic is especially troublesome because it is strong, durable, and non-biodegradable. Styrofoam and other plastics eventually break down into tiny particles that are now found in every remote corner of the ocean. They have been found in the guts of many animals that ingest them by mistake. Seabirds are particularly vulnerable. Larger plastic debris is also a threat. Sea turtles, seabirds, seals, and others are maimed or killed after getting entangled in plastic fishing line (Fig. 18.12). Many die with their digestive tract clogged with plastic bags and other debris.

Thermal Pollution

Seawater is often used as a coolant in power plants, oil refineries, and other industries, many of which are built along the coast. The heated water that results from the cooling process is pumped back to sea, causing alterations to the environment known as **thermal pollution.** Local warm pockets can be created in poorly mixed bays. Even though some fishes may be attracted to the site, such temperature increases are known to adversely affect some organisms. Higher temperatures also decrease the ability of water to dissolve oxygen. The effects of thermal pollution on marine life are especially pronounced in the tropics. In contrast to organisms living in temperate and polar regions, corals and some other tropical species normally live just below the highest tolerable temperatures. Reef-building corals are particularly sensitive (Fig. 18.3).

Saline brines from desalination plants that are used to obtain fresh water from seawater are a major pollutant in the Persian Gulf and some other coastal regions. Brines are typically warmer than coastal waters and highly saline as well.

Thermal pollution results when heated water is pumped into the sea.

THREATENED AND ENDANGERED SPECIES

The alteration or destruction of habitats by humans may have another disastrous effect: driving species to their eventual disappearance, or **extinction,** from the face of the earth. Organisms become adapted to changes in the environment as a result of **natural selection.** If they cannot adapt, they go extinct. Extinction is therefore a natural consequence of the process of evolution. To make a distinction, some biologists refer to human-induced extinction as **extermination.**

Species that face extinction are classified as **rare** when they are not in immediate danger but are at risk, **threatened** when their numbers have become low, and **endangered** when in immediate danger of disappearing forever.

Marine species may be threatened by overexploitation for food, hides, and other products. Many species of fishes, sea turtles, and other marine animals are killed and discarded as fisheries by-catch (see p. 388). Habitat destruction, pollution, and the introduction of pests (see "Biological Invasions: The Uninvited Guests," p. 414) and diseases also place species at risk. The Steller's sea cow, a **sirenian,** is a shocking example of a marine animal that was rapidly exterminated because of unregulated hunting for food (Fig. 18.13).

Species are categorized as rare, threatened, or endangered when they face the possibility of extinction, or extermination.

Isotopes Different atomic forms of an element.
- Chapter 2, p. 32

Natural Selection The production of more offspring by those individuals in a population that are genetically best-adapted to the environment.
- Chapter 4, p. 79

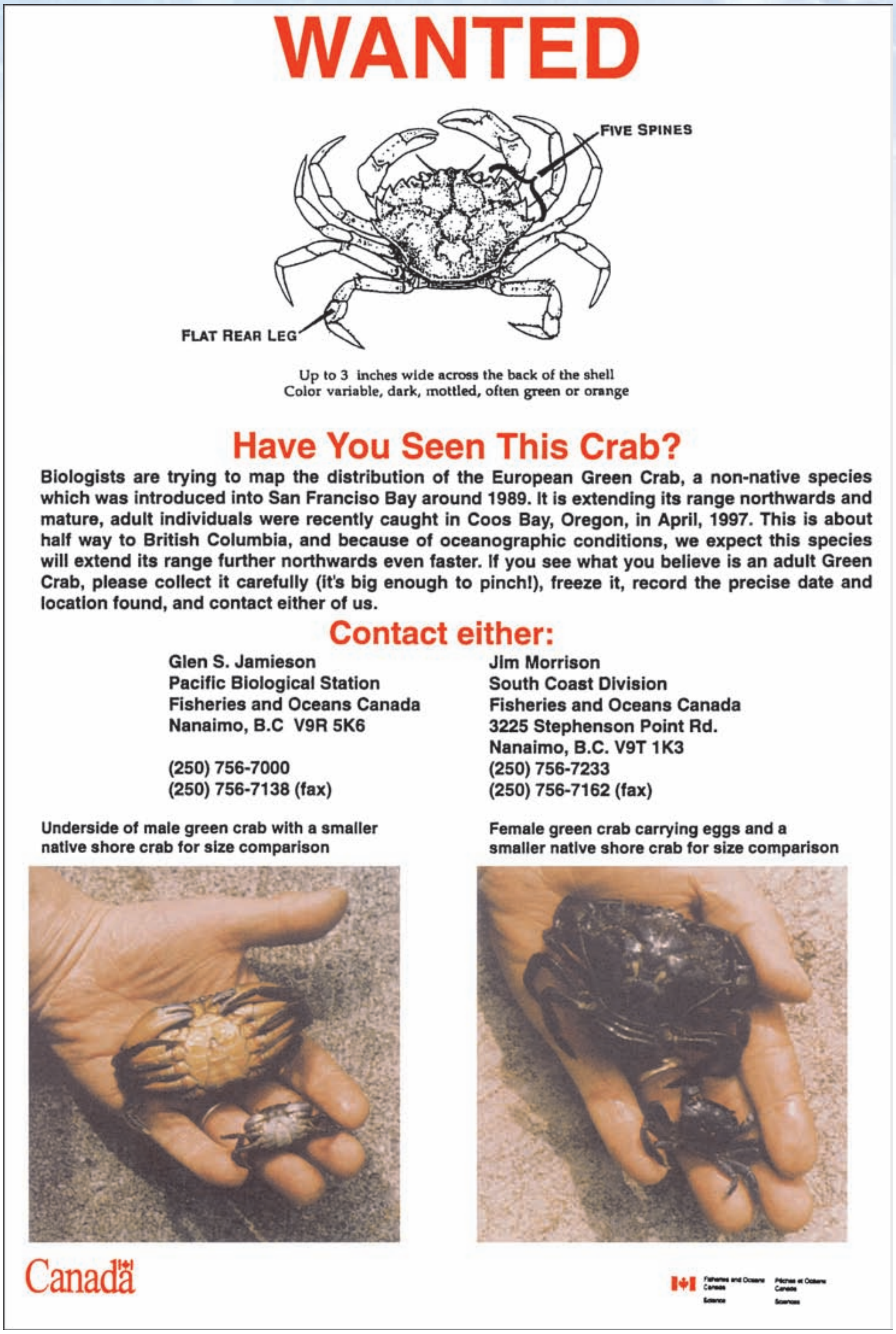
Sirenians A group of marine mammals collectively known as the sea cows having a pair of front flippers, no rear limbs, and a paddle-shaped tail.
- Chapter 9, p. 187

Biological Invasions: The Uninvited Guests

The deliberate or accidental introduction of **invasive species** in areas where they do not naturally occur can have devastating effects on the marine environment. One such effect has been the drastic reduction in the number of individuals belonging to **native,** or local, **species.** Invasive species, also known as **introduced** or **alien species,** often prove to be very strong competitors for food and space, and they can bring with them parasites that may infect native species. There has been an increase in the frequency of unwanted invasive marine species during the past few decades. It is the result of growth in shipping, the introduction of shellfish and fish for farming, and even the marine aquarium trade.

Bays and estuaries, especially those with busy ports, are particularly vulnerable. Seaweeds and invertebrates like sponges, barnacles, and sea squirts that grow as fouling organisms, which bore into or encrust on boats, pilings, and other underwater structures, have become established around the world. Many other species have been introduced as planktonic larvae in ballast water, which is used to fill ships' ballast tanks for stability. Others have been introduced with commercial fishery products, particularly shellfish. One good example is the Asian clam (*Potamocorbula amurensis*) that was accidentally introduced in San Francisco Bay, California, apparently as a direct result of the opening trade with China. These clams did not live in the bay in 1985, but by 1990 they literally covered whole sections of the bay's muddy bottom. As many as 10,000 clams per square meter carpet the bottom in some sections.

About 250 marine and estuarine invasive species have so far been found in San Francisco Bay. It's actually difficult to find a native species in some parts of the bay. Not only is San Francisco a busy port, but the bay is much disturbed. It is probably easier for an invasive species to become established when the environment is off balance. Many invaders do well in such unstable environments because they are often more tolerant than native species to wide fluctuations in factors such as salinity.



WANTED

FIVE SPINES

FLAT REAR LEG

Up to 3 inches wide across the back of the shell
Color variable, dark, mottled, often green or orange

Have You Seen This Crab?

Biologists are trying to map the distribution of the European Green Crab, a non-native species which was introduced into San Francisco Bay around 1989. It is extending its range northwards and mature, adult individuals were recently caught in Coos Bay, Oregon, in April, 1997. This is about half way to British Columbia, and because of oceanographic conditions, we expect this species will extend its range further northwards even faster. If you see what you believe is an adult Green Crab, please collect it carefully (it's big enough to pinch!), freeze it, record the precise date and location found, and contact either of us.

Contact either:

**Glen S. Jamieson
Pacific Biological Station
Fisheries and Oceans Canada
Nanaimo, B.C V9R 5K6**

**(250) 756-7000
(250) 756-7138 (fax)**

**Jim Morrison
South Coast Division
Fisheries and Oceans Canada
3225 Stephenson Point Rd.
Nanaimo, B.C. V9T 1K3
(250) 756-7233
(250) 756-7162 (fax)**

Underside of male green crab with a smaller native shore crab for size comparison

Female green crab carrying eggs and a smaller native shore crab for size comparison

Canada

The future of many marine species is at stake (Table 18.1). Perhaps the most widely known case is that of the whales (see "Whaling," p. 194), but there are many other examples. Giant clams (*Tridacna;* see Fig. 14.34) are taken for food and for their shells in such numbers that they have become rare or even locally extinct in most of the tropical Pacific. Marine snails like cowries (*Cypraea*) and cones (*Conus*), whose shells are eagerly sought by collectors (Fig. 18.14), have similarly disappeared from many areas. Intense commercial fishing to satisfy the growing markets for shark meat and fins, recreational fishing, and by-catch on longlines threatens many species of sharks. Sharks, like whales, reproduce slowly. It is

One of the more recent invaders to San Francisco Bay is the European green, or shore, crab (*Carcinus maenas;* see Fig. 7.38). It was first recorded in the bay in 1989, probably introduced as larvae in ballast water. It soon extended its range along stretches of the Pacific coast. The green crab has also been introduced, and has become a pest, in the northeastern coast of the United States, Australia, and South Africa. The green crab lives in a wide range of salinities. It is also a voracious predator, feeding on commercially valuable oysters and young Dungeness crabs.

Another notorious guest is a comb jelly (*Mnemiopsis leidyi;* see Fig. 7.12) that was accidentally introduced in the Black Sea. It normally occurs along the coasts of North and South America. First recorded in the Black Sea in 1982, it has become a monumental pest, practically taking over the sea. It not only competes with fish for zooplankton food but also feeds voraciously on fish eggs and larvae. Along with overfishing, its impact on the Black Sea fisheries has been devastating. Fish catches have sharply decreased, causing huge economic losses in the area. And yes, it has been found in San Francisco Bay, too!

More than 250 species of invertebrates and fishes have migrated from their original home in the Red Sea to the Mediterranean. These species migrated by way of the Suez Canal, which opened in 1869 to provide the shortest sea route between Europe and the Indian Ocean. The 160-km (100-mi) journey through the canal is getting easier because the high salinity of the lakes through which the canal passes has decreased, thus becoming less of a barrier to planktonic larvae brought in by tides. Most migrants have moved from the Red Sea to the Mediterranean because the high tide carries larvae further up the canal from the Red Sea. The migration of these invasive species has been called Lessepsian migration after the builder of the canal, Ferdinand de Lesseps. Migration between the Atlantic and Pacific oceans across the Panamá Canal has not taken place (except a species of barnacle) because only fresh water flows through the canal, killing any marine life that is brought in by the tide (also see Fig. 9.4).

Seaweeds have also been accidentally introduced. *Codium fragile,* a green seaweed, apparently brought over on oysters transplanted from Europe or the Pacific coast, has become a pest by growing in masses on rocks and oysters on the northeastern coast of the United States. *Caulerpa taxifolia,* a green seaweed that grows into branches as long as 3 m (9 ft), was accidentally introduced in the Mediterranean from the Caribbean in 1984. This fast-growing seaweed has spread rapidly, particularly in the western Mediterranean, where it smothers seagrasses and other native species and depletes oxygen from the bottom. Unfortunately, the bright-green seaweed is widely used in marine aquaria. Its importation into the United States was banned in 1999, but in 2000 it was found in shallow water off Southern California, perhaps the result of someone emptying a fish tank into a storm drain. Other invasive seaweeds include *Caulerpa brachypus,* which smothers and kills corals in Florida, and several red algae introduced in the Hawaiian Islands (species of *Kappaphycus* and *Eucheuma denticulatum;* see Fig. 14.14).

Inland waters have not escaped uninvited guests. The small freshwater zebra mussel (*Dreissena polymorpha*) was introduced, probably in ballast water from Europe, in the Great Lakes. It was first found in 1988 but quickly spread. It is now found in all five Great Lakes in North America, the Hudson River estuary, and the Ohio River drainage basin as well. The clam has taken over the shallow-water bottom in many areas. It has caused costly damages because it disrupts water supplies by invading water-intake pipes.

The intentional introduction, or **transplantation,** of species for commercial purposes can also bring in invasive species. The Japanese oyster (*Crassostrea gigas*) was introduced as spat, or young individuals, on the Pacific coast of North America. It was a successful transplantation in the sense that the oyster is now of significant commercial value. Unfortunately, many species living on the spat shells were also introduced. A nasty invasive species is an oyster drill (*Ceratostoma inornatum*), a marine snail that preys on oysters and other native bivalves. Also introduced was *Sargassum muticum,* a Japanese brown seaweed that is now established from British Columbia to Southern California. The same species has also been introduced in England, probably with transplanted Japanese oysters. Species of cordgrass like *Spartina alterniflora,* from the Atlantic coast of North America, have caused problems in many regions worldwide when transplanted by spreading over mudflats, oyster beds, and eelgrass beds (see “Biological Control of Invasive Cordgrass,” p. 276).

Another potential source of invasive species is the release into the ocean of marine aquarium fishes. Aquarium owners are suspected of releasing venomous lionfishes (*Pterois;* see Fig. 8.10*c*) and other Pacific aquarium fishes into the Atlantic coast of the United States. The seemingly harmless introductions may be horror stories in the making. It remains unknown if these fishes have been permanently established but lionfishes are known to reproduce in their adopted home. Local fishes and invertebrates cannot recognize these predatory fishes, and harmful parasites may have also been introduced.

It is difficult to prevent the introduction of uninvited guests. One possible option is to control or regulate the use of ballast water. The use of filtered or sterilized ballast water or the exchange of ballast water in mid-ocean far from land has been explored. The transplantation of species from different geographical regions must also be strictly regulated. Rigorous studies of the biology of the species involved and those in the proposed new locations should also be undertaken before such transplantations are carried out.

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feared that many shark species may be pushed to the brink of extinction in a decade or two. All seven species of sea turtles are endangered. Adults as well as eggs have been exploited for food and tortoiseshell (Fig. 18.15; also see “The Endangered Sea Turtles,” p. 180). Their nesting sites have been overrun by development, and they drown in fishing nets.

Seabirds have not fared well, either. Overfishing has been responsible for a decline in the number of seabirds in many parts of the world as a result of the decline in food. Longline fishing kills around 100,000 albatrosses (*Diomedea*) a year in Antarctic waters alone. Nineteen of the 22 species of albatrosses are threatened or endangered, some critically so.

Table 18.1 Endangered and Threatened Marine Species

Group of Marine Animals	Red List of Threatened Species, 2006[1] (Critically Endangered, Endangered, and Threatened Species)	CITES List of Species Threatened with Extinction, 2006[2]	CITES List of Species Vulnerable to Exploitation, 2006[3]
Corals and other cnidarians	3	0	All scleractinian, black, blue, organ-pipe, and hydrozoan corals
Other invertebrates	12	0	0
Marine molluscs	79	0	9
Marine fishes	795	2	48
Sea turtles	7 (all)	7 (all)	0
Marine iguana	1	0	0
Seabirds	297	5	1
Sirenians	4 (all)	3	0
Seals, sea lions, walrus	31	3	8
Sea otter	1	1	0
Polar bear	1	0	0
Whales, marine dolphins	77	24	1

[1] Compiled by the International Union for Conservation of Nature and Natural Resources.

[2] Appendix I, Convention on International Trade in Endangered Species of Wild Flora and Fauna.

[3] Appendix II, Convention on International Trade in Endangered Species of Wild Flora and Fauna.

Many marine mammals that have low reproductive rates also face extermination. Some species of seals, sea lions, and the walrus have been decimated for their skins, meat, blubber, or the precious ivory of their tusks. Monk seals *Monachus* are endangered; one species, the Caribbean monk seal *M. tropicalis*, is most probably extinct. The number of Steller sea lions *Eumetopias jubatus* has sharply declined in the northwestern Pacific. The sea otter (*Enhydra lutris;* see Fig. 9.12) had made a comeback but its numbers have been declining and it is still threatened (see "Kelp Communities," p. 296). Manatees (*Trichechus;* see Fig. 9.13) and the dugong (*Dugong dugon*), the smaller cousins of the extinct Steller's sea cow, are both in danger of extinction.

Many marine species are at risk of being exterminated because of unregulated exploitation and other anthropogenic impacts. Whales, sea turtles, manatees, and other marine mammals are especially imperiled.

CONSERVING AND ENHANCING THE ENVIRONMENT

There is increasing evidence for the loss of biodiversity through the disappearance of species as a result of the loss and degradation of habitats (see "Biodiversity: All Creatures Great and Small," p. 215). Conservation of biodiversity aims at the conservation of a vast number of species, their habitats, and entire communities, not merely the preservation of a limited number of endangered species.

Conservation

The protection, or conservation, of coastal areas from the advancing wave of development is of crucial importance. A growing human population (see Fig. 17.2) and the increasing demands of practically everyone exert continuous pressure on the natural environment. The apparent conflict between economic development and the protection of coastal resources, though especially intense in developing countries, occurs everywhere. Development should be **sustainable,** that is, it must meet the needs of today without affecting the ability of future generations to meet their needs. Laws have been passed by many governments, but there is still a lot to be done. **Coastal management** aims at promoting the wise use of our coasts while ensuring that the benefits of this use can be sustained for future generations. The multiple use of coastal resources

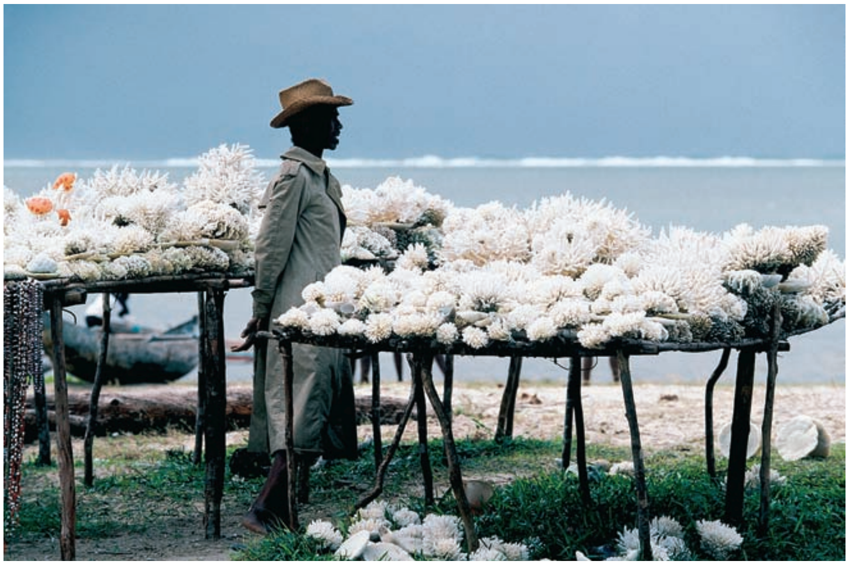


FIGURE 18.14 Reef-building corals for sale to tourists at a beach in Madagascar.

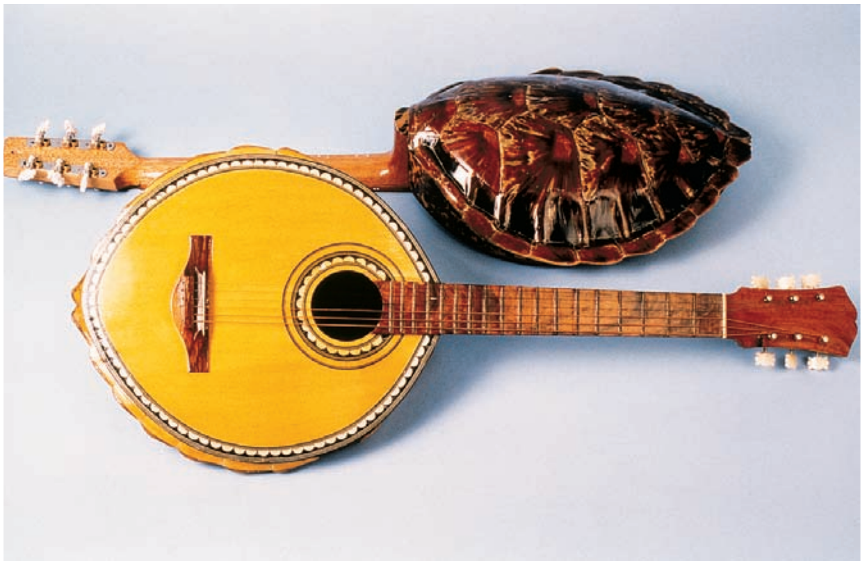


FIGURE 18.15 One of the many types of tortoiseshell products that are regularly confiscated by the U.S. Fish and Wildlife Service. They are part of the illegal multimillion-dollar world trade in endangered species.

and the need to manage them calls for judicious planning to accommodate the often conflicting interests of developers, fishers, surfers, power-plant builders, beachgoers, and nesting seabirds. Coastal management deals with issues as varied as historical preservation, beach access, military uses, tourism, and water quality.

Efforts to stop the deterioration of the marine environment include conservation and effective coastal management.

Conservation efforts include many local, national, and international projects (Fig. 18.16) and legislation dedicated to the protection of species and environments. Oil drilling, for instance, has been banned along some coasts, as in California. Commercial fisheries are regulated by national governments, partly as a result of the establishment of **exclusive economic zones,** or **EEZs,** and by international commissions (see "Managing the Resources," p. 389). Unfortunately, many stocks are still being harvested at levels above **maximum sustainable yields** (see Fig. 17.10). Governments have also established **marine protected areas** for the protection and management of areas of ecological significance. The National Estuarine Reserve Research System of the United States, for example, designated 17 reserves in 14 states and Puerto Rico protecting almost 1,200 km^2 (3,100 mi^2) of estuaries, salt marshes, and mangrove forests. The Great Barrier Reef in Australia, the Florida Keys, and other areas around the world have been designated marine protected areas. The world's largest marine reserve, the Northwestern Hawaiian Islands Marine National Monument, was created in 2006. It protects pristine coral atolls, which are inhabited by several threatened and endangered species, as well as the surrounding waters, a total area of around 360,000 km^2 (nearly 140,000 mi^2) northwest of the main Hawaiian Islands. Twenty-nine marine protected areas were also designated along the central coast of California the same year. Marine protected areas are usually richer in both the number and the abundance of species compared with unprotected waters around them. There is some evidence that protected areas benefit surrounding waters through either "seeding," in which the offspring of individuals inside the protected area settle elsewhere, or "spillover," in which juveniles and adults move out of the protected area. Only a tiny fraction of the ocean, 0.5%, is protected, however.

Groups and organizations like the World Wildlife Fund, the United Nations Environment Programme, The Nature Conservancy, and the Sierra Club play an active role in conservation through education, the sponsoring of projects, and even lobbying for legislation.

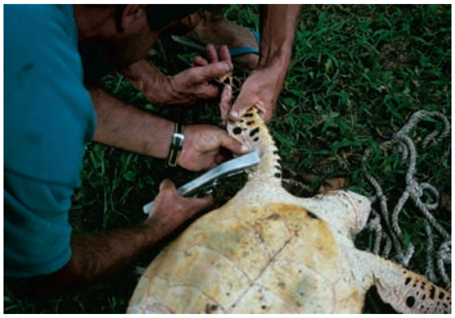


FIGURE 18.16 Biologists tagging a hawksbill turtle (*Eretmochelys imbricata*) in Papua New Guinea to learn more about its migrations and habits. Papua New Guinea is the only place with breeding grounds for six species of sea turtles. This photograph was taken at Wuvulu Island, where sea turtles are common because the inhabitants do not eat turtle meat and eggs as a result of religious restrictions.

Restoration of Habitats

Another strategy for improving the quality of the environment is to help habitats recover from modifications caused by habitat destruction and pollution. **Habitat restoration** helps recovery from stress by transplanting, or restocking, key species from healthier areas. The loss of priceless salt marshes and mangrove forests through landfilling or the building of boat marinas can be at least partially compensated for by creating or improving a similar but unstressed habitat elsewhere. These efforts, of course, assume that the new location meets the physical requirements (such as tides, salinity, and the type of substrate) for the development of a healthy biological community.

Successful examples of habitat restoration include the transplantation of cord grass (*Spartina*), one of the dominant plants of salt marshes, and of mangrove seedlings. Introduced species of cord grass, however, have taken over habitats normally inhabited by native species (see "Biological Control of Invasive Cordgrass," p. 276). Restoring salt marshes has been facilitated by reopening blocked connections to the open sea in order to restore tidal flow. Channels are constructed and

Exclusive Economic Zone (EEZ) A zone 200 mi (370 km) wide along the coast, in which nations have exclusive rights to fishing and other resources.
- Chapter 17, p. 390

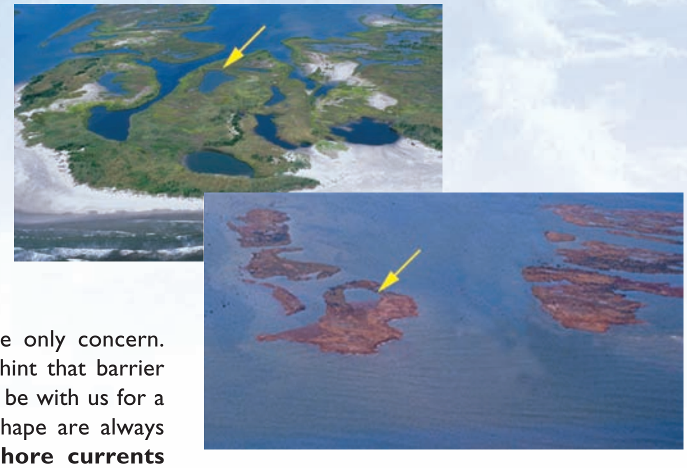
Sand on the Run, or What to Do with Our Shrinking Beaches

Sandy beaches constitute one of our most valuable coastal resources. Millions use them for recreation, and their importance as a tourist attraction is evident from Atlantic City to Waikīkī. Unfortunately, beaches have been shrinking and disappearing everywhere.

Sandy shores happen to be among the most restless of all marine environments. Sand shifts, so disruptions like storms, hurricanes, winds, and currents periodically modify the shore. The Atlantic and Gulf coasts of the United States are protected by **barrier islands**—long, low, sandy islands that run parallel to the coast. This long stretch of islands constitutes one of the world's most splendid sandy beaches. Barrier islands are characteristic of shores bordering wide continental shelves. They were formed as sea levels began to rise between 12,000 and 14,000 years ago (see "Climate and Changes in Sea Level," p. 33). Waves and wind began pushing bottom sediments and formed bars on the flat shelf. Sand bars eventually formed barrier islands, which migrated toward the shore as the sea level rose.

The value of barrier islands goes beyond protecting coastline by absorbing the stress of hurricanes and currents. Their **sand dunes** are inhabited by salt-resistant plants and land animals. Seabirds use them as nesting sites. Barrier islands may include salt marshes, seagrass meadows, freshwater sloughs, and even forests. Florida's barrier islands feature mangrove forests. Untouched barrier islands, however, are becoming rare. Bridges and roads have made some more accessible, and as a result they have been overrun by development.

Development is not the only concern. Their origin may give us a hint that barrier islands were not planned to be with us for a long time. Their size and shape are always changing. Wind and **longshore currents** erode their seaward side by continually shifting sand from one tip to the other, north to south in the eastern United States. Channels between islands may fill up, and previously damaged islands may be eroded away, as in the case of Hurricane Katrina in 2005.



Effects of Hurricane Katrina, August 2005 (bottom), on a barrier island off the Louisiana coast.

Not everybody realizes that sandy beaches and barrier islands will not tolerate permanent structures for too long. Seawalls, breakwaters, jetties, and groins may be built as a safeguard but often make the problem worse. Erosion may be controlled by encouraging the natural development of dunes or by planting vegetation that helps stabilize the sand. Replenishing sand by bringing it periodically from offshore is one expensive, but temporary, way to save a beach. This is what is being done in highly urbanized Southern California, where rivers, which once brought in sand to the shore, now end behind dams or have been transformed into concrete-bottomed channels. Efforts to manage beaches and barrier islands, however, may only disrupt the natural coastal processes that sooner or later will triumph over our ingenuity.

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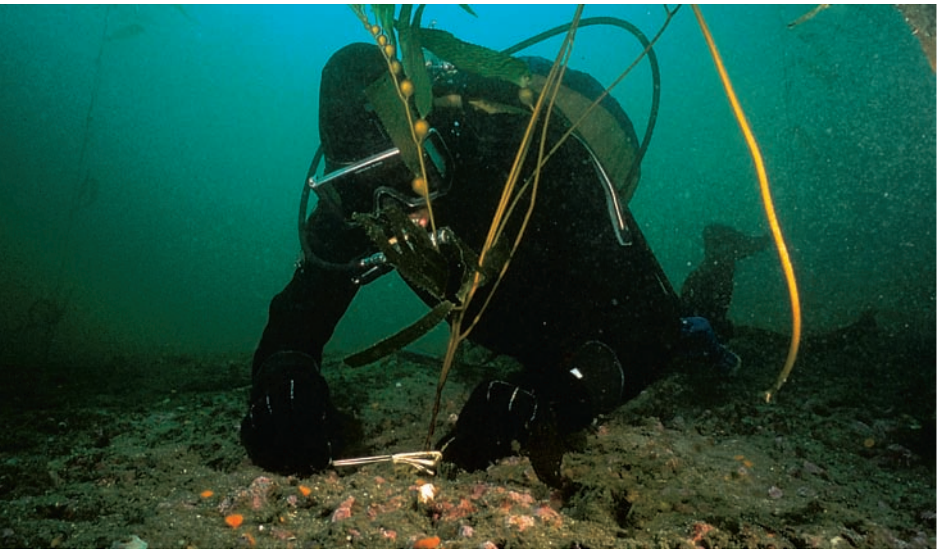
accumulated sediment dredged. Tides slowly bring in the larvae of other components of the community. Young giant kelp (*Macrocystis*), with their root-like holdfasts tied to concrete blocks or to submerged nylon lines, have been used to help restore kelp forests (Fig. 18.17). New techniques in the transplantation of coral and seagrasses, promise the reseeding of damaged reefs and seagrasses. Seabirds are even being attracted to old nesting grounds by using painted decoys and solar-powered tape recorders that play bird calls!

FIGURE 18.17 Restoration of marine habitats has included the transplantation of young giant kelp plants (*Macrocystis pyrifera*) into areas where kelp forests have diminished or vanished.



Habitat restoration is nevertheless a poor alternative to preventing the degradation of marine environments. Restoration rarely if ever restores habitats to their natural condition, and it is usually expensive.

Conservation of marine environments includes the establishment of marine protected areas and the restoration of habitats.

Artificial Reefs

Fishing can be greatly enhanced by building **artificial reefs.** The irregular surfaces and the hiding places provided by the reefs attract fishes, lobsters, and other life, as well as anglers and divers. Shellfish and seaweeds

Five Simple Things You Can Do to Save the Oceans

Our impact on the health of the oceans is much more serious than we often assume. We all impact the oceans, no matter how far we live from the seashore. You can do a lot to help save the oceans and the rest of the planet. Here are five simple things inspired by *50 Simple Things You Can Do to Save the Earth* by the Earthworks Group and *50 Ways to Save the Ocean* by D. Helvarg.

1. *Take care of the environment.* If you go to the seashore or go snorkeling or diving, do not disturb the environment in any way. Respect natural habitats. Return any overturned rocks to their original positions. Leave all forms of life where they are. Ask questions when buying fish or ordering it at a restaurant: Where is it from and how was it caught? Buy fish certified as sustainably caught (check for the blue or white label from the Marine Stewardship Council). Eat lower on the food chain (shellfish, squid) and less or no swordfish, tuna, shark, and grouper. If you go fishing, target species that are abundant and not those that are overfished, even if it's legal. Know the regulations and take only what you really need for food. Return undersized fish. If you travel overseas, don't buy products made from endangered or threatened species like tortoiseshell or ivory, which may come from walruses. Corals and shells should be left alone, and alive, in their natural home. Be sure to tell merchants you object to their sale of shells, corals, sand dollars, and other marine life, which were most probably collected alive and killed for sale. If you buy fishes, corals, and other marine life for your marine aquarium, be sure to check before buying if they were obtained in an environmentally responsible, sustainable way. Clean after your pets. Their feces may carry parasites that, if washed to sea, can infect marine mammals as well as humans.
2. *Save energy.* Saving on energy keeps carbon dioxide, a greenhouse gas that promotes global warming and acidification of seawater, out of the atmosphere. Get out of the car. Use public transportation or a bike more often. Get rid of your SUV (and save 12 tons of greenhouse emissions a year!) and get a smaller car or a hybrid. Tailpipe pollutants add to the nitrogen nutrients that cause eutrophication of coastal waters. *Save electricity.* Most power plants still burn coal to produce electricity, releasing more carbon dioxide (an electric drier produces an average of 3.6 pounds of carbon dioxide a day but drying clothes on a clothesline produces none!) plus more nitrogen compounds as well as mercury. Saving gasoline and electricity also reduces the need for oil and thus the threats of more offshore oil drilling and oil spills.
3. *Dispose of hazardous materials properly.* The list of toxic chemicals we use is endless, from heavy metals and pesticides to even PCBs. Reduce your use of toxic chemicals at home, which are in discarded computers and electronics, batteries, motor oil, paints, cleaners, and many other types of household trash. Dumping them on the ground, in the trash can, or down storm drains or letting them accumulate in land fills is likely to pollute wetlands, the ocean, or rivers, which drain into the ocean. Flushing them down the drain simply adds them to sewage, which may ultimately flush, untreated, into the ocean. Your local recycling center can tell you how to recycle hazardous materials.
4. *Recycle plastics. Use less of them.* Reduce the risk of plastics being washed to sea by recycling them. Don't forget to pick up any plastic you may have left around the beach. Cut open those six-pack rings before disposal; you don't know where they may end up. Properly dispose of snarled fishing line; never toss it at sea or on shore. Use reusable canvas bags to do your shopping instead of plastic bags, thousands of which get blown or thrown to the sea every day around the world.
5. *Get inolved. Keep informed.* Be aware of and keep up with environmental issues. Read, ask questions, listen carefully. Numerous organizations, societies, and agencies are committed to help save our planet. Hear what they have to say and sponsor them. Make your voice heard. Vote for the oceans and the planet. Support marine protected areas.

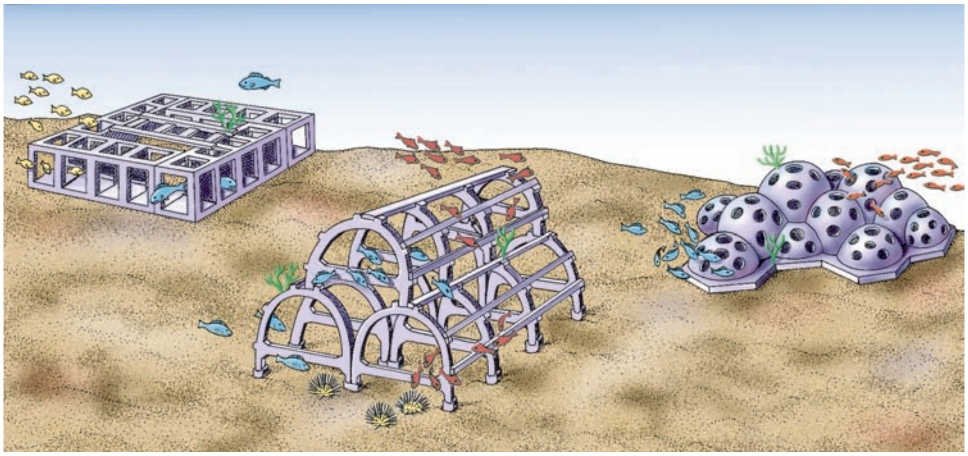


FIGURE 18.18 Artificial reefs can be built of various types of prefabricated concrete blocks.

like kelp can thrive on their surfaces. Everything from concrete blocks, discarded tires, and toilets to scuttled ships, useless battle tanks, an old 727 jet, and custom-made frames and structures have been used to build artificial reefs around the world (Fig. 18.18). Hundreds have been built in Japan, where *tsukiiso,* or reef-construction, has been successful in increasing commercial yields of fishes, abalone, sea urchins, and seaweeds. It has been argued, however, that artificial reefs may only concentrate fishes and wildlife in one spot, making them easier to catch and contributing to their depletion.

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Wastes from duck farms used to wash into two shallow-water bays on Long Island, New York. The wastes, rich in nutrients such as nitrate and phosphate, polluted the water. What do you suppose was the immediate effect of the pollutants? Can you speculate on the likely effects on the commercially valuable shellfish of the area?
2. It is found that a chemical present in effluents coming from a factory is being stored in the tissues of herring, a plankton-feeding fish. What type of observations and possible experiments would you suggest to find out if the chemical is biodegradable? What is the significance of finding out if the chemical is biodegradable or not?
3. Tourism and its effects (for example, pollution from hotels and the impact of boats and tourists on fragile habitats) often clash with conservation efforts. Sometimes, however, tourism can help. The economic impact of banning the hunting of harp seals in eastern Canada has been compensated for, in part, by the influx of tourists who now go to see the seals. Can you think of other examples? What recommendations can you make to minimize the impact of tourism on unspoiled marine environments?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Burdick, A., 2005. The truth about invasive species. *Discover,* vol. 29, no. 5, May, pp. 34–41. Not all introduced species are as undesirable as they may seem to be.

Duncan, D. E., 2006. Pollution within. *National Geographic,* vol. 210, no. 4, October, pp. 116–143. Fears about the health effects of pollutants such as PCBs, lead and other chemicals are growing.

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Graham-Rowe, D., 2006. How did it come to this? *New Scientist,* vol. 191, no. 2561, 22–28 July, pp. 39–41. Dismantling old oil tankers to prevent pollution releases toxic materials.

Krajick, K., 2004. Medicine from the sea. *Smithsonian,* vol. 35, no. 2, May, pp. 50–59. Marine organisms from many habitats are being investigated as sources of new medications.

Mallin, M. A., 2006. Wading in waste. *Scientific American,* vol. 294, no. 6, June, pp. 52–59. Disease-causing microbes pollute beaches and food sources as a result of unchecked development.

Mee, L., 2006. Reviving dead zones. *Scientific American,* vol. 295, no. 5, November, pp. 78–85. Dead zones, like in those in parts of the Black Sea, may recover by decreasing nutrient runoff from land.

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Wright, K., 2005. Our preferred poison. *Discover,* vol. 26, no. 3, March, pp. 58–65. Because of its many uses and great toxicity, mercury is a major pollutant.

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Leslie, H. M., 2005. A synthesis of marine conservation planning approaches. *Conservation Biology,* vol. 19, pp. 1701–1713.

Odell, J., M. E. Mather, and R. M. Muth, 2005. A biosocial approach for analyzing environmental conflicts: a case study of horseshoe crab allocation. *BioScience,* vol. 55, no. 9, pp. 735–748.

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Traditional fishing in the Gulf of Thailand.

19

CHAPTER

The Oceans and Human Affairs

We close our review of life in the oceans by briefly outlining the ways the ocean has molded, affected, or influenced human cultures. Chapter 17 looked at our use of marine resources, Chapter 18 at how we are affecting the health of the ocean. Now we turn to the other side of the coin to see how the ocean has influenced us, a global issue with wide-ranging implications.

OCEANS AS BARRIERS AND AVENUES

Once upon a time, people believed that our planet was flat and that sailing beyond the horizon meant falling into the gaping mouths of sea monsters (Fig. 19.1). The peoples of the world were separated from each other by unknown continental masses or by the great expanses of uncharted waters. The oceans served as barriers between cultures. Even the few kilometers of channel that separates England from mainland Europe had an isolating effect and helped define and distinguish English culture. The cultures of Ireland, Madagascar, Japan, and other island nations were similarly affected.

Few people risked venturing beyond the horizon. There were, however, exceptions. For centuries Arab sailors regularly sailed across the western Indian Ocean. The Vikings crossed the North Atlantic during the ninth and tenth centuries, as did Basque whalers not long after. Polynesian double canoes sailed the great expanses of the Pacific, and Chinese sailors crossed the Indian Ocean and may have reached the easternmost shores of the Pacific. It was not until the fifteenth century, however, that the European voyages of discovery began to change the ancient and medieval view that the world was flat.

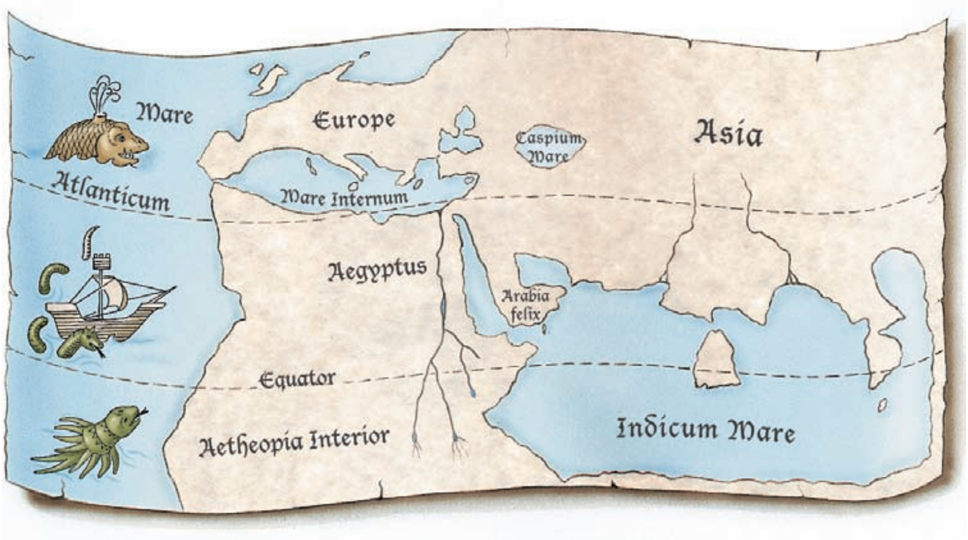


FIGURE 19.1 Fifteenth-century cartographers, greatly influenced by the geography of Ptolemaeus (second century A.D.), thought the earth was flat. Notice that, according to this map, circling Africa to reach India is impossible because the Indian Ocean is landlocked.

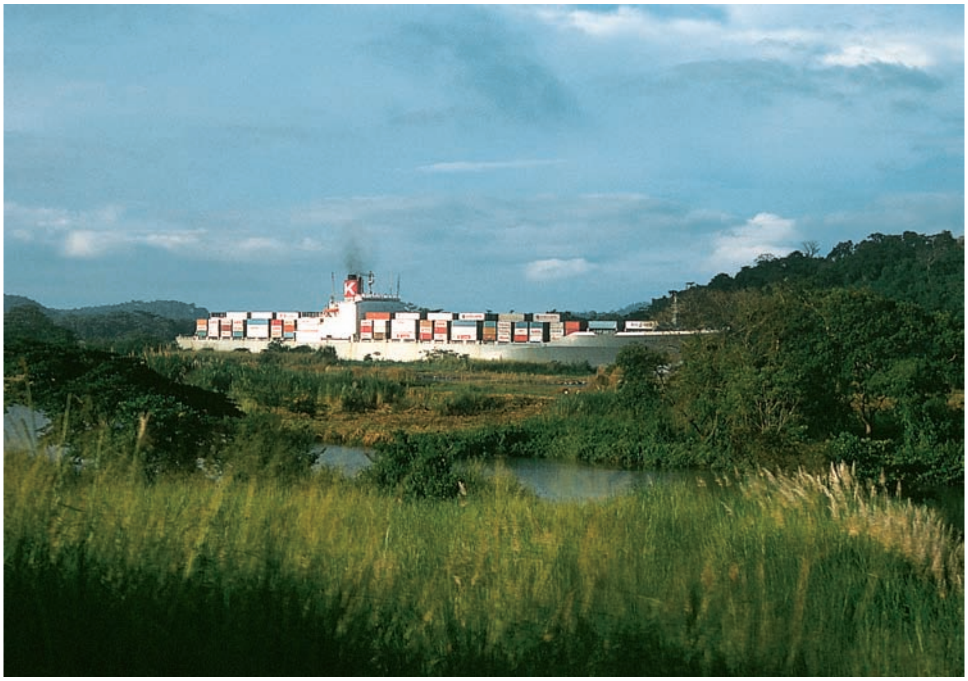


FIGURE 19.2 This giant containership, seemingly making its way across land, is actually crossing from the Pacific to the Atlantic Ocean by way of the Panamá Canal. New containerships, able to carry as many as 11,000 standard containers, are too big to fit through the canal.

The quest to discover new lands beyond the sea in Europe was pioneered by the Portuguese, who sailed around the southern tip of Africa and on to India by the late fifteenth century to take a share of the profitable spice trade (see "Tall Ships and Surface Currents," p. 50). Also looking for a shorter way to the Orient was Christopher Columbus, who first crossed the Atlantic in 1492. Unlike the Vikings, who landed in America centuries before, Columbus' "discovery" was soon known by everyone. Many other seaborne explorers followed, not all looking for spices (see "The History of Marine Biology," p. 2). Between 1480 and 1780, these explorers opened all oceans and, except for most polar regions, few coastlines remained unexplored. The oceans then became very powerful avenues of culture and commerce, war, and disease. Colonialism was carried across the oceans, and so were immigrants, slaves, religions, languages, traders, scientific discoveries, and ideas.

> The oceans, which before the age of discovery and exploration helped effectively isolate the peoples of the earth, eventually became an avenue for change.

Today the oceans are vital freeways that link world economies by transporting raw materials and manufactured goods. Shipping remains the cheapest way to move large quantities of goods over long distances, so most international trade moves by sea. Globalization of economies has strengthened the growth of marine trade. Seaborne trade grew dramatically after World War II. It decreased by around 10% during the 1980s but only, because of a drop in crude oil shipments, which still accounts for the largest volume of seaborne trade. Businesses that deal in commodities such as iron ore, coal, and grain rely heavily on shipping. The enormous variety of goods being shipped has led to the development of vessels specialized in the transport of such exotic cargoes as liquified gas, livestock, and wine. A large percentage of maritime cargo now moves by large steel containers that are carried to the docks by trucks and lifted by cranes into giant containerships (Fig. 19.2). Cargo is then unloaded at the final destination without ever having been touched by human hands.

The oceans are no longer the avenue of choice for the transport of people, except for short distances along the coast. Jets now transport people between the continents, but large passenger ships have found a new life carrying tourists to sunny coasts.

Nowadays, the oceans are also connected by rubbish and pollutants. The oil from the Middle East, lobster tags from Newfoundland, shampoo bottles from Greenland, and ice-cream containers from Brazil that were washed ashore on a beach in Ireland bear witness to the sad reality.

OCEANS AND CULTURES

Our association with the ocean probably goes back to our early beginnings. It has been suggested that some of the early stages of human evolution were spent on the seashore and that our ancestors were coastal inhabitants who frequently waded in the water searching for food. The evidence for this, so goes the argument, is our scanty hair, a relatively streamlined body, and the presence of a layer of fat for insulation—adaptations also found in cetaceans! Most scientists dismiss this hypothesis. Nevertheless, the ocean undoubtedly influenced the human cultures that developed along coastal regions from prehistoric times.

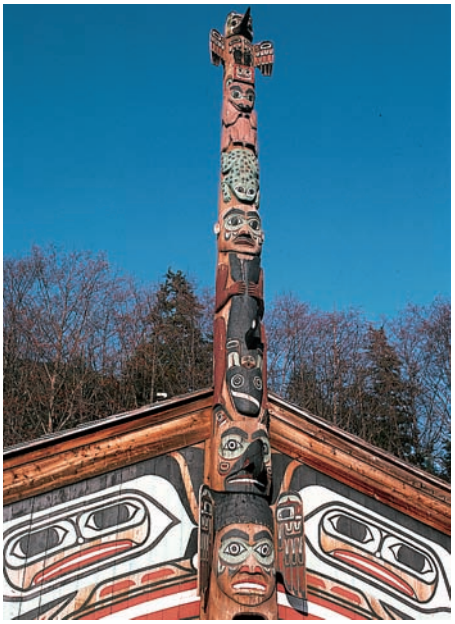


FIGURE 19.3 Totem poles carved by the native inhabitants of the Pacific Northwest often include marine motifs such as halibut, killer whales, and sea otters.

Culture, which includes the components of the environment created by humans, is reflected in a multitude of ways. It encompasses objects like tools, ornaments, and dwellings and immaterial things like customs, institutions, and beliefs. An intimate relationship with the ocean has molded many cultures around the world. Some anthropologists refer to them as **maritime cultures.**

Excavations of prehistoric waste dumps and shell middens, the accumulation of leftover shells, give evidence of the importance of marine life as food and of the advantages of living near the seashore. Fishhooks were one of the first tools made by humans. Remains of fishes, sea turtles, seabirds, and pinnipeds are often found in prehistoric deposits. They have allowed archaeologists to describe the food habits, the diet changes, and sometimes the overexploitation of food resources by ancient cultures.

Humans then began to learn to fish using nets, traps, and other, more sophisticated techniques. The extraction and trading of salt was of tremendous importance, influencing the development of cities and states. Boats were subsequently improved, allowing fishers and salt traders to roam farther from shore.

Fishing was very important for many coastal Native Americans. Nowhere was this more evident than among the northwest coastal Indians that inhabited the Pacific shores from southern Alaska to northern California. Their livelihood depended to a great extent on salmon, marine mammals, shellfish, and other marine life. These coastal peoples knew the seasonal changes in abundance and the migration patterns of the species that fed them. Some tribes were even aware that **red tides** made mussels poisonous. Marine life also provided a basis for religious beliefs. The salmon, for instance, was for some tribes a supernatural being who took the shape of a fish and sacrificed itself every year to help humans. The fish spirits returned to their homes at sea to be transformed back into fish if their bones were thrown back into the water. Rituals were carried out to prevent salmon from being offended and thus refusing to return and swim up the rivers to be caught for food. Marine life also provided inspiration for wood carvings, such as totem poles (Fig. 19.3). Shells from abalone and other gastropods were used in making masks and ornaments.

The Inuit and other peoples native to the Arctic fished and hunted whales and other marine mammals from *kayaks,* one- or two-person boats made of seal or walrus skins, or *umiaks,* larger boats also made from skins. Native folklore is rich in stories of hunting incidents in which the hero is helped by spirits arising from the sea. Though native cultures have changed, some continue to follow traditional ways of fishing and hunting (see "Effects of Climate Change on Arctic Peoples," p. 427).

The Seri Indians of northwestern Mexico regularly used the seeds of eelgrass *Zostera* from the Gulf of California (see Fig. 13.15) as a traditional food source—the only known case of a grain being harvested from the ocean. Eelgrass is now harvested only occasionally by the Seri. Its flour is used to make a gruel that is flavored with honey, cactus seeds, or sea turtle oil. In the old days, toasted grains were used to cure children's diarrhea. The dry eelgrass was used as roofing and to make dolls. A deer or bighorn sheep scrotum filled with dry eelgrass made a ball for children to play with.

The early Polynesians, Micronesians, and other peoples of Oceania had the whole Pacific Ocean as their backyard. As a result, they developed extraordinary skills as navigators. Unlike Europeans, they were not afraid of the ocean. They settled the farthest reaches of the Pacific, from New Zealand and the Mariana Islands to Hawai'i and Easter Island. For this remarkable feat, they relied on double-hulled canoes that were carved from trees and secured with coconut fiber (Fig. 19.4).

The ocean and its creatures also provide images and symbols for the folklore and art of the peoples of Oceania (see Fig. 1.1). According to legend, New Zealand was discovered when Polynesian fishers pursued an octopus that stole their bait. The ocean has a chief role in their creation myths and other aspects of their mythology. In some cultures a giant clam is said to have been used in the making of heaven and earth. In others a great spotted octopus holds heaven and earth together. There are also countless stories involving marine life—tales of porpoise girls, pet whales, and shark gods falling in love with locals.

The sea helped mold many of the maritime cultures that developed in coastal regions around the world.

Red Tides Blooms of some dinoflagellates, cyanobacteria, and other organisms that discolor the water and produce toxins that, if accumulated in shellfish, cause *paralytic shellfish poisoning* in humans.

- Chapter 15, p. 331

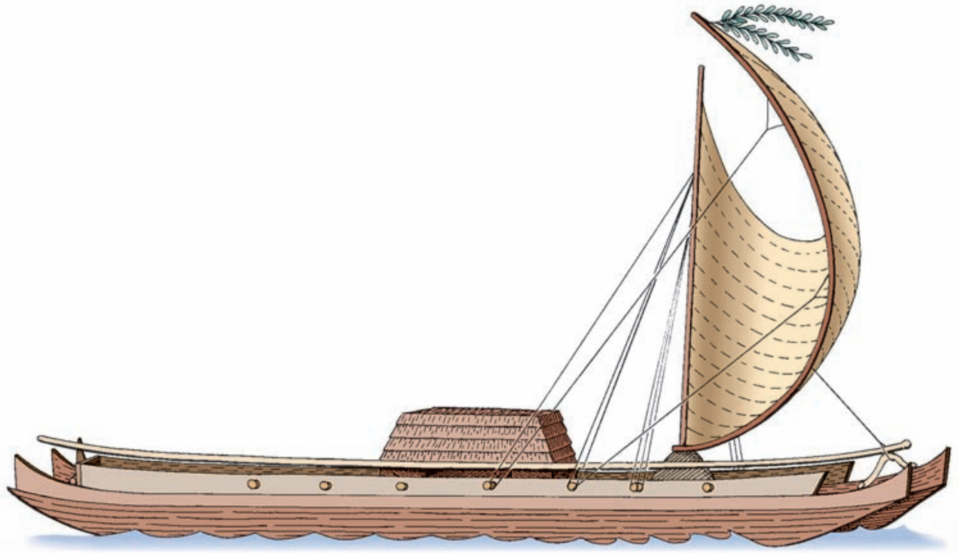


FIGURE 19.4 *Wa'a kaulua,* a Hawaiian double-hulled canoe.

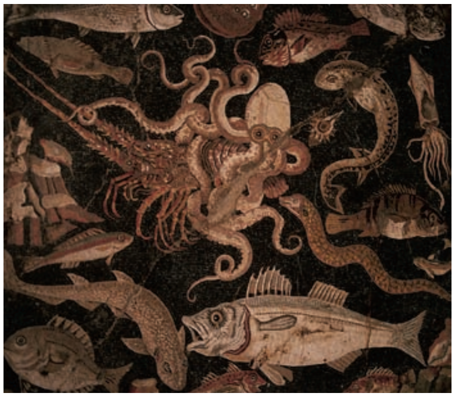


FIGURE 19.5 The Romans often used marine motifs in mosaics to decorate floors and walls.

Ancient seafaring cultures also emerged in the Mediterranean and the Middle East. Egyptians, Phoenicians, Greeks, Persians, Romans, and other ancient mariners fished, traded, and made war with each other at sea. They were often inspired by the sea (Fig. 19.5). Many of their shipwrecks have yet to be discovered (see "Marine Archaeology," p. 425).

Fishing and commerce remained the basis of coastal economies in Europe during the Middle Ages. The Baltic Sea herring fishery, for example, was the livelihood of the Hanseatic League, a thriving federation of Baltic and North Sea ports. When the fishery collapsed in the fifteenth century, so did the league.

England, the Netherlands, and Portugal owed much to seaborne trade and sea power for their emergence as leading nations during the late Middle Ages and early modern times (Fig. 19.6). In many ways they followed the example of Venice and Genoa, the great rival seaports in Mediterranean trade. Fishing, trade, and naval power, in particular, began to play other important roles. By stimulating shipbuilding, they strongly encouraged exploration, science, and technology.

"Those who rule the sea rule the land" soon emerged as a motto of the emerging nation-states. Echoes of Lepanto, the defeat of the Spanish Armada, Trafalgar, Navarino, and other legendary sea battles still ring in our ears as heroic sagas. *The Influence of Sea Power upon History,* a book written in 1890 by the American naval officer and historian Alfred T. Mahan, emphasized the importance of sea power. This book was influential in persuading major powers to build modern fleets in the years before World War I. Mahan's predictions were quickly confirmed: In 1905 the Russian Empire was crippled when the Japanese sank their Pacific fleet. The Jutland, Midway, Coral Sea, and other World War I and II naval battles further proved the strategic importance of the oceans in modern warfare.

Since the birth of "gunboat diplomacy," nations have continued to use sea power to exert their influence by defending their local or global interests. Missile-carrying nuclear submarines, long-range bomber planes, and nuclear missiles have replaced battleships as a first-strike force for the superpowers. The control of sea lanes, critical to world economies, and the defense of oil, fishing, and other coastal resources will ensure the continuous importance of naval power for many nations.

In the meantime, many of the maritime cultures that managed to survive have been greatly modified and transformed. Only traces may remain of times when life depended on the cycles of the ocean and on the food caught from it.

Some maritime cultures still survive. The traditional knowledge, customs, and laws of these cultures are seen as valuable tools in protecting fisheries and biodiversity in local seas. Fishing villages of maritime peoples who are still faithful to a unique

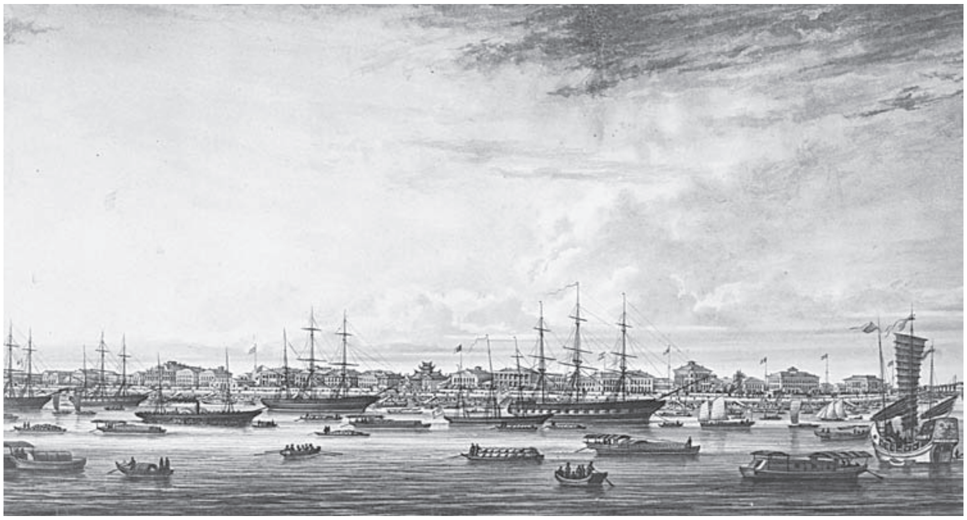


FIGURE 19.6 Shanghai became China's leading port and the base for commercial penetration by the Western powers after the city was opened to unrestricted foreign trade in 1842. This 1860 drawing shows the great variety of ships and vessels used in the transoceanic and local trade.

Marine Archaeology

The discovery, salvage, and interpretation of humankind's cultural heritage that remains undersea is the aim of a relatively new field, **marine archaeology.** New tools, like scuba diving and remotely operated undersea vehicles, have allowed marine archaeologists to reveal secrets that had remained concealed by sediment at depths beyond our reach.

Marine archaeology as a modern science was born in 1960 when archaeologists excavated a 3,000-year-old ship off the Mediterranean coast of Turkey. Before that time, the chance recovery of sunken artifacts was occasionally carried out by sponge fishers, not by trained archaeologist-divers. Underwater digs have since been investigated around the world. The oldest so far seems to be that of a Bronze Age ship loaded with fascinating artifacts that sank off the southwestern coast of Turkey 3,500 years ago.

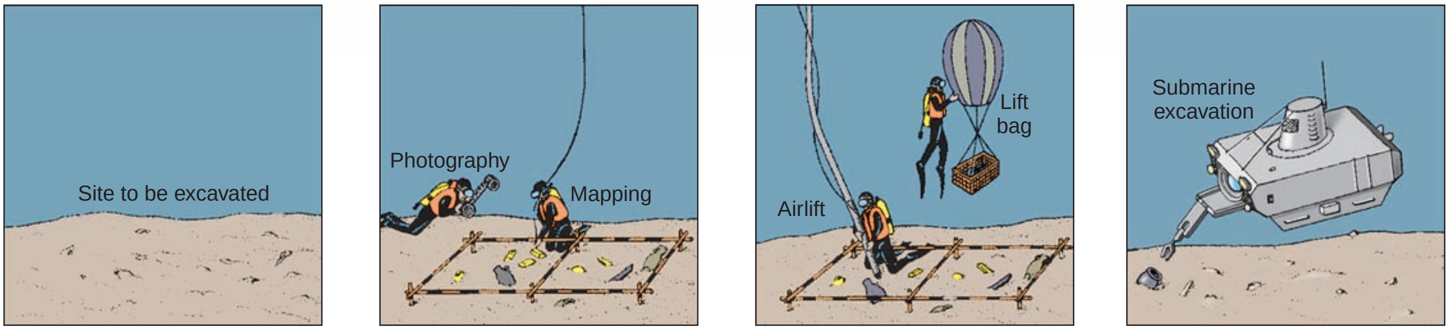
These underwater digs have provided invaluable information about ancient cultures: ship construction, life aboard ship, trade and discovery routes, and naval warfare. Tools, utensils, footwear, weapons, coins, and jewelry found on sunken ships have given us details of the products that were traded, food habits, and other aspects of everyday life.

Underwater sites may also yield art treasures, gold, and other valuables. Already a few priceless bronze Greek sculptures have been recovered from the Mediterranean. Some wrecks of Spanish galleons, as well as more modern ships, hide a fortune in gold, coins, and jewelry. The plundering of wrecks for valuables is a major problem because archaeologically significant sites may be damaged or dispersed.

Shipwrecks may be located by analyzing old documents and charts. Shallow-water wrecks have been discovered by divers attracted by half-buried hull fragments, an anchor, or a pottery amphora that stored olive oil or wine in better days. Underwater surveying of wrecks involves dives, underwater photography and television, air photography, and charting of the site using a grid system. More sophisticated techniques are also being used. Side-scan sonars use reflected sound waves to survey large sections of the ocean floor, whereas sub-bottom sonars can profile sites covered with sediment. A computer-controlled system called sonic high-accuracy ranging and positioning system, or SHARPS, provides archaeologists with three-dimensional maps of sites. A remotely controlled underwater vehicle sends live pictures to a vessel that beams them to a satellite in charge of relaying them to museums and institutions to be studied by experts. The image thus moves from the bottom to the water surface to space to land thousands of kilometers away in a matter of seconds!

Marine archaeologists are also involved in excavating towns and harbors that became submerged. They can provide valuable data on the economy and the use of technology of past cultures. Port Royal in Jamaica, which sank as a result of an earthquake in 1692, is an example of such a submerged dig. So is the now-submerged port of Cesarea Maritima, a Roman city on the coast of Palestine.

Sometimes sunken ships remain intact, as in the case of the *Vasa,* a Swedish warship that sank during its maiden voyage in 1628. It rested quietly in Stockholm harbor until 1961, when it was lifted whole from a depth of 33 m (108 ft). The wreck had been preserved by cold water and thick mud. Luckily, wood-eating shipworms were absent because of the low salinities of the Baltic. Another case is that of the *Mary Rose,* an English warship that sank in 1536. Its starboard half, the only surviving part, was raised in 1982 after yielding valuable artifacts. The turret and cannons from the *Monitor,* a Civil War ironclad that lies 67 m (220 ft) below the surface off Cape Hatteras, have been raised. Sections of the *Titanic,* which lies some 4,000 m (13,000 ft) under the sea, may be next!



Some techniques used by marine archaeologists.

livelihood and who depend on the ocean for their survival can be found throughout the islands of the Pacific and in isolated spots such as the coast of Labrador, the Faeroe Islands, and the island of Tristan da Cunha in the South Atlantic. Some have managed to survive along coasts no longer classified as isolated (Fig. 19.7). The Bajaus, or "sea gypsies," of the southern Philippines and North Borneo are boat dwellers who, like their ancestors, have followed a nomadic life at sea, fishing and diving for pearls. Korea's women divers still dive for edible marine life as a livelihood. The Kuna Indians of the Caribbean coast of Panamá literally cling to several hundred tiny offshore islands, some built out of coral and filled in by the Kuna themselves. And then there are the Dutch, a maritime people by tradition who still manage to inhabit land they have reclaimed from the bottom of the North Sea by using dikes and canals. A large portion of their densely populated country actually lies below sea level. Many modern societies still include fishers, fish and shellfish farmers, sailors, commercial divers, and other occupational groups that depend on the ocean (Fig. 19.8). As such, they are regarded as maritime subcultures.

The imprint of the oceans on humankind still survives in our daily lives in cultural elements that transcend food, commerce, politics, and war. The sea and its lore endures in the work of

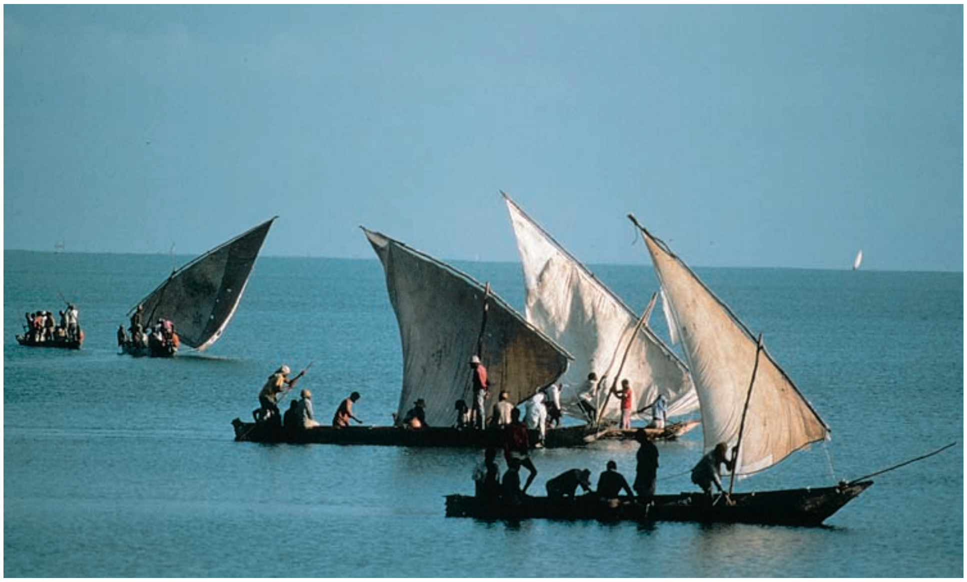


FIGURE 19.7 Fishers and traders have used the traditional Arab *dhow* for centuries. These fishers in Tanzania, East Africa, are using a small, one-masted version. *Dhows* still sail between India and ports in the Arabian Peninsula, Red Sea, and East Africa along what is considered the world's oldest commercial sailing route.

FIGURE 19.8 Sailors like this man mending fishing nets in Malaysia belong to a maritime subculture that remains tightly linked to the rhythms of the ocean.

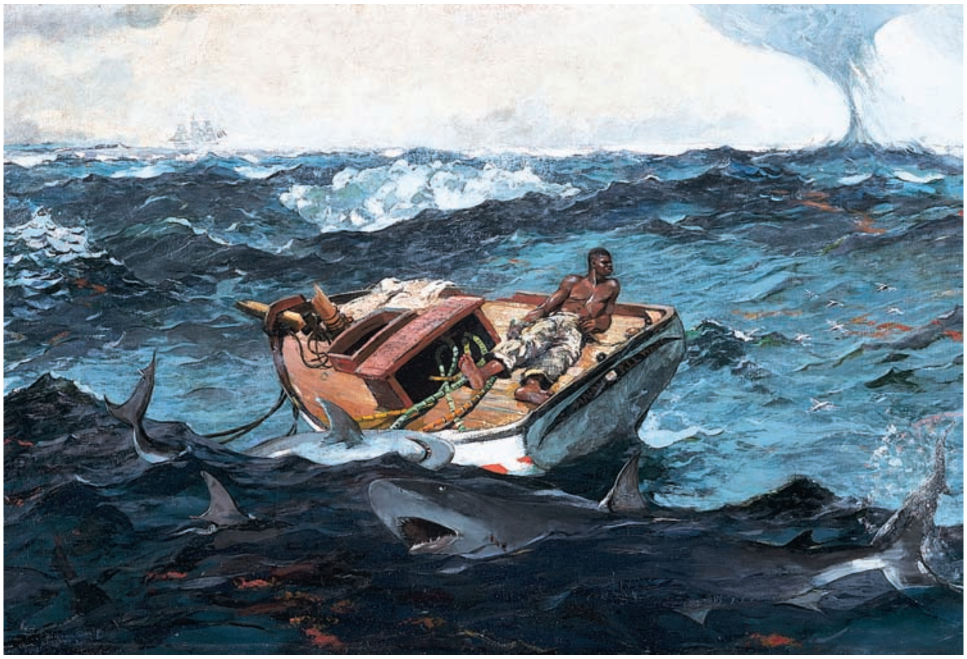


FIGURE 19.9 The *Gulf Stream* (1899), an oil painting by Winslow Homer, an American painter much influenced by marine subjects.

writers, painters (Fig. 19.9), and musicians such as Conrad, Melville, Hemingway, Neruda, Turner, Monet, and Debussy. The sea has even inspired architects (Fig. 19.10).

OCEANS AND RECREATION

Another legacy from the ocean is **recreation.** Rising standards of living and increased leisure time, particularly in the developed countries, have opened up opportunities for the recreational enjoyment of the ocean.

Practically anybody who can afford it can now fly to a faraway beach or take a cruise among once remote paradise islands. **Ecotourism** in spots like the Galápagos and Antarctica offers tours for divers and nature lovers. Catering to those seeking the sun and fun of the sea has developed into a giant tourist industry, one that keeps afloat many national and local economies. Whale-watching cruises now employ many fishers left without employment, and locals may opt to protect marine life they see as a source of income. In many areas, however, tourism has displaced fishing and other traditional activities and even endangered species like sea turtles. Water pollution is often a result of the extra millions of gallons of sewage generated by development. The destruction of habitats from the building of hotels and other facilities and the increase in the number of divers and boat traffic are other harmful side effects.

Recreation for many people revolves around water sports like snorkeling, scuba diving, sailing, water skiing, and surfing. Surfing alone is for some a way of life, a subculture of its own. Together with marine sports fishing (see "Marine Life as Items of Commerce and Recreation," p. 394), ocean sports provide relaxation and support a thriving recreation industry.

EYE ON SCIENCE

Effects of Climate Change on Arctic Peoples

Global warming (see "Special Report: Our Changing Planet," p. 231) is predicted to first and most harshly affect the peoples inhabiting the Arctic regions of the world. The anticipated increases in average temperatures and the subsequent reduction in sea ice will be particularly severe along the coasts of the Arctic Ocean, a region where the Inuit and other aboriginal peoples have carved out a precarious existence for thousands of years. The melting of Arctic sea ice is actually advancing at a rate faster than originally predicted.

The consequences of global warming are especially worrisome to the communities of the Canadian Arctic, a vast region of islands, glaciers, and fjords. The shrinkage and eventual disappearance of the coastal sea ice in many areas will lead to the loss of habitat to Arctic marine life like the polar bear, harp seal, and walrus, which are important sources of food, shelter, clothing, and tools for the Inuit. This change in marine life will severely disrupt traditional hunting by the Inuit. Also being affected are land animals like the caribou, which are also used for food and many kinds of implements. Warmer temperatures and the thawing of the permanently frozen soil are already damaging buildings and disrupting transportation. The loss of coastal sea ice will also increase exposure of coastal communities to storms. Ice melting may soon allow the opening of a Northwest Passage shipping route linking the Atlantic with the Pacific, a positive development for commerce but one that will threaten traditional ways of life and increase the danger of oil spills.

The vulnerability of the Canadian Inuit when facing the transformation of the Arctic environment has triggered concern about their future. A multidisciplinary research program, ArcticNet, was created to study not only the environmental costs of climate change in the Canadian Arctic but also of the socio-economic consequences to the Inuit. The program involves research teams from several Canadian universities and government agencies, Inuit organizations, and teams from Greenland, Russia, the United States, and several other European and Asian nations. ArcticNet also maintains oceanographic observatories in the Canadian and Siberian Arctic Ocean. Automated instruments record temperature, salinity, nutrients, phytoplankton biomass, and marine mammal vocalizations. A Canadian Coast Guard ship, the *Amundsen,* is transformed by ArcticNet into a floating clinic that visits coastal villages in the Canadian Arctic to study the health of the Inuit. Longitudinal studies in which the same patients are interviewed and examined every five years allow epidemiologists to document how the health of the inhabitants is impacted by climate change and modernization. A network of eight research stations is being created. The stations, which stretch from the northern limit of forests to as far north as Ward Hunt Island, a rocky spot 800 km (500 mi) from the North Pole, will allow long-term studies by scientists. Four of the stations will be owned by Inuit communities. The stations will also monitor global distillation, which is responsible for the high levels of pollutants from southern latitudes that condense in polar regions (see "PCBs and Other Toxic Organic Chemicals," p. 410) and a health hazard to Arctic inhabitants.

Perhaps the most serious problem for the Inuit is the availability of wildlife, which is expected to disrupt the preparation of traditional foods and lead to the use of alien foods, hence directly affecting health and at the same time bringing on cultural changes. The implication are being investigated by teams of researchers that gather data by interviewing Inuit hunters and elders. Its ultimate aim is to analyze the impact that landscape change may have on daily activities and how an alteration in the social benefits of hunting may lead to changes in the way of life.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

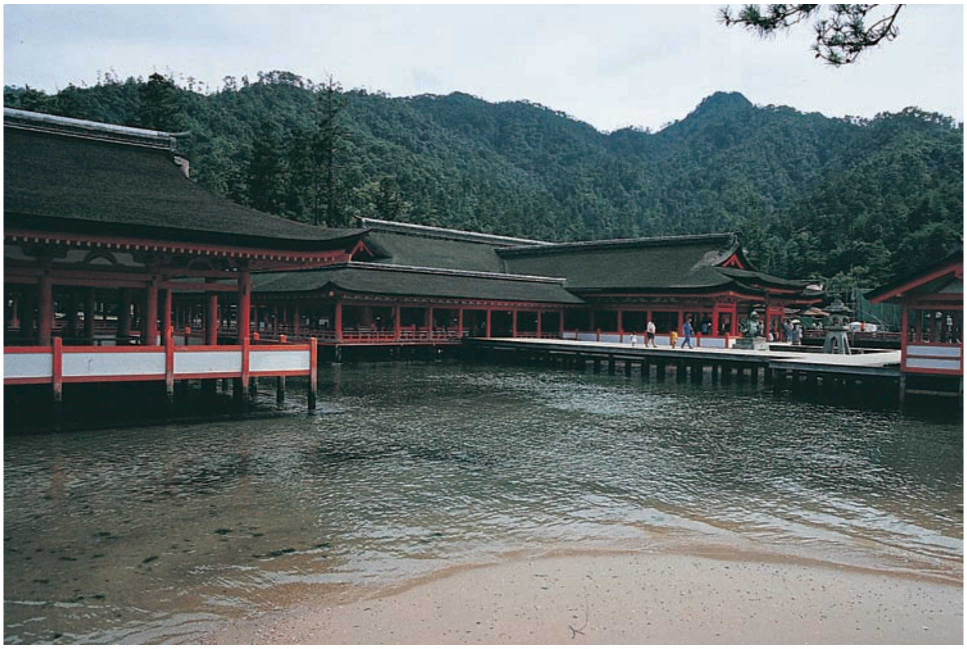


FIGURE 19.10 Architecture inspired and influenced by the sea: the *Itsukushima-jinja* shrine in Japan. Both the shrine and its famous gate, or *torii,* were designed to appear to float on water at high tide.

Recreational opportunities offered by the ocean influence the way many people spend their leisure time and those who depend on the tourist industry for a living.

PROSPECTS FOR THE FUTURE

It is impossible to predict what lies ahead for our world ocean. Optimists have visions of cities built underwater or on floating islands, food from mariculture, unlimited energy from the water and seabed, and no pollution to speak of. Most, however, are less confident. They point out that our impact on the marine environment will escalate as the world's population expands. Modern technology will lead to new means of exploitation, and for resources never imagined before. The prospects are therefore not very promising. The destruction of habitats, pollution, and the extinction of species will certainly escalate if no drastic measures are taken. Perhaps even more alarming is the possibility of a rise in sea levels as a result of **global warming** (see "Rolling the Dice: Climate Change," p. 231).

The oceans, the heritage of all humankind, must be safeguarded to save them from overexploitation and pollution. This has been one of the aims of the **United Nations Conference on the Law of the Sea (UNCLOS),** the 1982 treaty that culminated many years of deliberations by the many nations that were represented. Only relatively few nations have ratified the treaty, though many have implemented some of the provisions of the treaty.

The treaty, for example, led to the establishment of the **exclusive economic zones (EEZs)** that extend a nation's economic interests 200 nautical miles (370 km) from the coast. This agreement has had significant consequences for the management of marine resources, particularly fisheries (see "Managing the Resources," p. 389). Nations owning tiny islands and reefs barely above high water can now claim large portions of the surrounding seabed, which may hold untold riches in oil or minerals. Such is the case of the Paracel and Spratly islands in the South China Sea, now claimed by several nations in the region. The treaty also allows free passage beyond a 12-nautical-mile (22-km) **territorial sea** around a nation's shores. Unimpeded surface and underwater transit is guaranteed through straits that fall within the territorial sea of one or more nations. This includes the straits of Hormuz (in the Persian Gulf), Bering, and Gibraltar, all of which have great strategic importance. The treaty also calls for nations to enact laws and regulations to prevent and control pollution. It also guarantees the freedom to undertake scientific research in the high seas.

The Third United Nations Conference on the Law of the Sea initiated a series of international agreements in an effort to define the use of the oceans by all nations. They included the establishment of exclusive economic zones.

Other international agreements have attempted to solve other problems. The **U.N. Conference on Environment and Development** at Rio de Janeiro, known as the Rio Earth Summit of 1992, is one example. It resulted in an agreement to preserve biodiversity on the planet (see "Biodiversity: All Creatures Great and Small," p. 215). One commitment was to protect the interests of the traditional fisheries of indigenous people.

From the early beginnings the oceans have influenced humankind by providing food and avenues of commerce and culture. It is clear, however, that the relationship has been reversed. The oceans are now being influenced by humankind—the destruction of habitats, pollution, overfishing, and the potential effects of global warming. Limited progress has been made, but the future of the oceans doesn't seem to be very bright after all. Is it too late to say, "Let's wait and see?"

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. Most maritime cultures either are long gone or have been radically modified by others. Which elements of a rapidly changing maritime culture do you predict would be the first to disappear? Which would tend to remain unchanged the longest?
2. The Third United Nations Conference on the Law of the Sea made no provisions for Antarctica. Some of the land is probably rich in resources like oil, so the eventual exploitation of the land is probably inevitable. Several nations have already established claims, sometimes overlapping each other, to sections of the continent. How would you deal with these claims? Would you give first preference to nations, like Argentina or New Zealand, that claim geographical proximity to the continent, or to those, like Norway or Britain, that arrived at the claimed land first? How can resources be exploited if it is decided that the land does not belong to any particular nations?

For Further Reading

Some of the recommended reading may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

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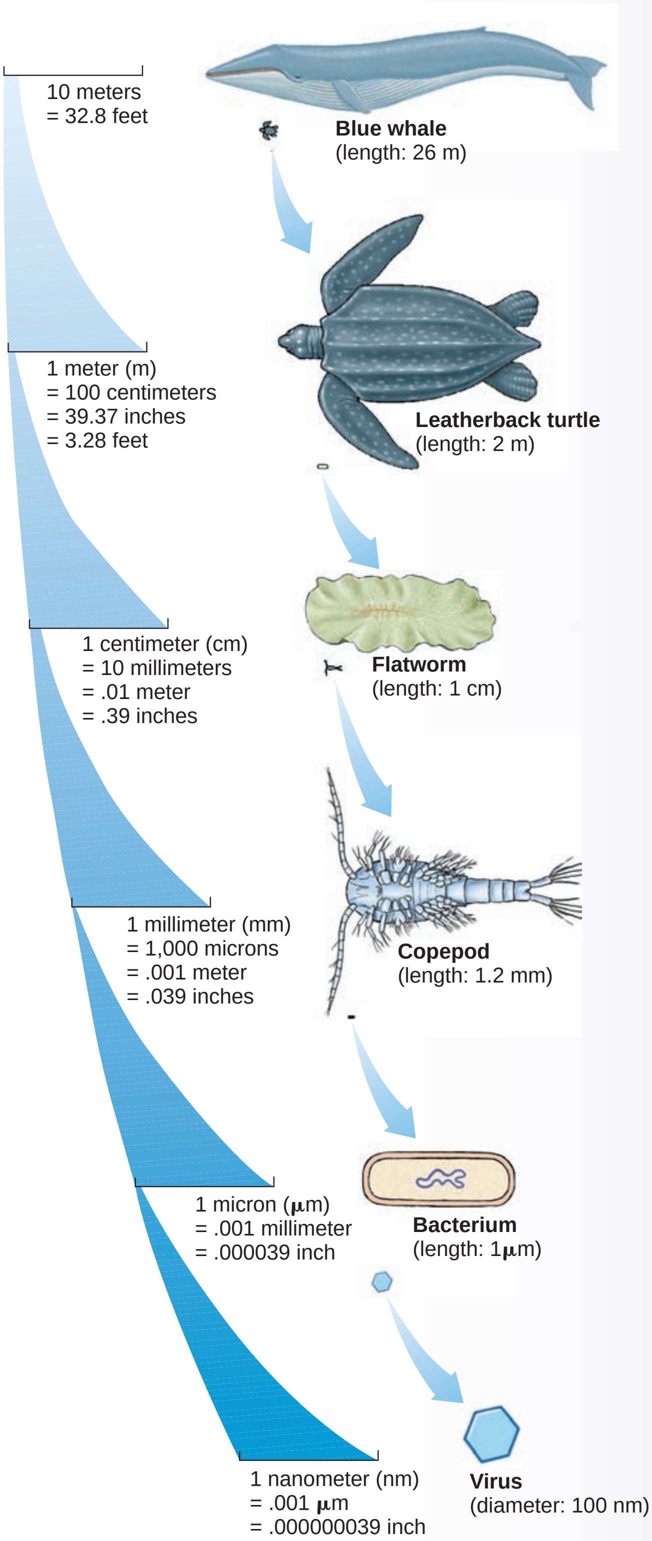
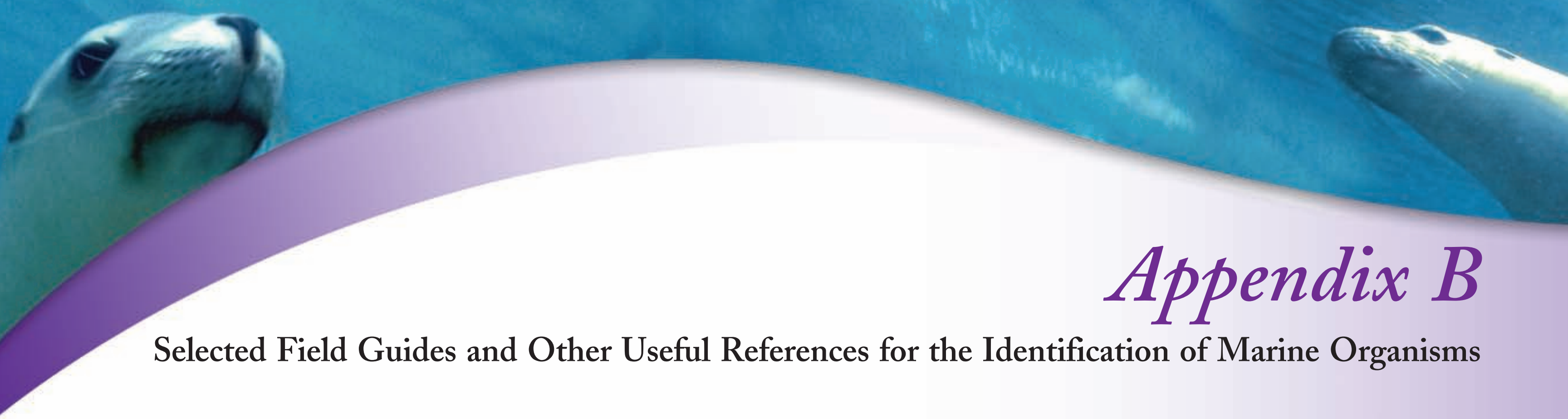
Appendix A

Units of Measurement


10 meters
= 32.8 feet
Blue whale
(length: 26 m)
1 meter (m)
= 100 centimeters
= 39.37 inches
= 3.28 feet
Leatherback turtle
(length: 2 m)
1 centimeter (cm)
= 10 millimeters
= .01 meter
= .39 inches
Flatworm
(length: 1 cm)
1 millimeter (mm)
= 1,000 microns
= .001 meter
= .039 inches
Copepod
(length: 1.2 mm)
1 micron (µm)
= .001 millimeter
= .000039 inch
Bacterium
(length: 1µm)
1 nanometer (nm)
= .001 µm
= .000000039 inch
Virus
(diameter: 100 nm)



Appendix B

Selected Field Guides and Other Useful References for the Identification of Marine Organisms

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Glossary

Words in boldface are defined separately in the glossary. Other key terms are given in italics.

A

abiotic A non-living (physical or chemical) component of the environment. Compare **biotic.**

aboral surface The surface opposite the mouth (or *oral surface*) in **cnidarians, comb jellies,** and **echinoderms.**

abyssal plain The nearly flat region of the deep-sea floor.

abyssal zone The bottom from a depth of approximately 4,000 m (13,000 ft) to 6,000 m (20,000 ft) (Fig. 10.12).

abyssopelagic zone The **pelagic** environment from a depth of 4,000 m (13,000 ft) to 6,000 m (20,000 ft) (Fig. 10.12).

acorn worms (enteropneusts) See **hemichordates.**

active continental margin A **continental margin** that is colliding with another plate and as a result is geologically active (Fig. 2.22). Compare **passive continental margin.**

active transport The transfer of substances across membranes by a cell against a *concentration gradient.*

adenosine triphosphate See **ATP.**

adductor muscle One of two muscles that close a bivalve's shells (Fig. 7.23*d*).

aerobic respiration The chemical process involved in the release of **energy** from organic matter (Fig. 4.5):

$$\underset{\text{(glucose)}}{\text{organic matter}} + O_2 \rightarrow \underset{\hookrightarrow \text{energy}}{CO_2} + H_2O$$

agar A commercially important **phycocolloid** extracted from **red algae.**

alga (pl. **algae**) Any of several groups of **eukaryotic, autotrophic protists** that lack the structural features (true leaves, roots, and stems) of plants.

algal ridge A ridge of **coralline algae** that is found on the outer edge of some **coral reefs.**

algal turf A dense growth of often filamentous **algae.**

algin A **phycocolloid** extracted from **brown algae** that is widely used in food processing.

alternation of generations A reproductive cycle in which a **sexual** stage alternates with an **asexual** one, as in the case of a **gametophyte** alternating with a **sporophyte.**

ambergris Undigested material that accumulates in the intestine of the sperm whale.

ambulacral groove Each of the radiating channels of **echinoderms** through which **tube feet** protrude.

amino acid One of the 20 nitrogen-containing molecules that make up **proteins.**

amphibians (class *Amphibia*) **Vertebrates** that lay their eggs in fresh water: frogs, salamanders, and allies.

amphipods A group of small, laterally compressed **crustaceans** that includes *beach hoppers* (Fig. 7.32) and others.

ampulla (pl. **ampullae**) Each of the muscular sacs that extend inside the body opposite the **tube feet** of **echinoderms.**

ampulla (pl. **ampullae**) **of Lorenzini** One of several sensory structures in the head of sharks that detect weak electric fields (Fig. 8.3).

anadromous Marine fishes that migrate to fresh water to breed. Compare **catadromous.**

anaerobic bacteria **Bacteria** that do not need oxygen.

anaerobic respiration The breaking down of organic matter by organisms in the absence of oxygen. Also see **aerobic respiration.**

anal fin The last **ventral** fin of fishes (Fig. 8.8).

angiosperms See **flowering plants.**

animals Members of the kingdom *Animalia*, which consists of **heterotrophic, eukaryotic,** multicellular organisms.

annelids See **segmented worms.**

anoxic Lacking oxygen. Compare **hypoxic.**

antenna A sensory appendage on the head of **arthropods.**

anthozoans (class *Anthozoa*) **Cnidarians** whose life cycle consists of a complex **polyp** and no **medusa.**

anthropogenic impact Disturbance to the natural environment caused by humans.

apneustic breathing Breathing pattern shown in many marine mammals that involves deep breaths followed by exhalation.

appendicularians See **larvaceans.**

aquaculture The farming of marine and freshwater organisms. Also see **mariculture.**

archaea (sing. **archaeum**) **Prokaryotic,** unicellular microorganisms in the domain *Archaea.*

Aristotle's lantern The set of jaws and associated muscles used by **sea urchins** to bite off food (Fig. 7.48).

arrow worms (**chaetognaths;** phylum *Chaetognatha*) Planktonic **invertebrates** characterized by a streamlined, transparent body (Fig. 7.43).

arthropods (phylum *Arthropoda*) **Invertebrates** that have jointed appendages and a **chitinous,** segmented **exoskeleton.**

ascidians See **sea squirts.**

asexual (vegetative) reproduction The type of reproduction that takes place without the formation of **gametes.** Compare **sexual reproduction.**

asthenosphere The layer of upper **mantle** that lies below the **lithosphere** (Fig. 2.3).

atoll A **coral reef** that develops as a ring around a central **lagoon** (Fig. 14.23).

atom The smallest unit into which an **element** can be divided and still retain its properties.

ATP (adenosine triphosphate) A molecule that stores **energy** and releases it to power chemical reactions in organisms.

autotroph An organism that manufactures its own organic matter by using **energy** from the sun or other sources. Compare **heterotroph.**

auxospore The resistant stage of **diatoms** that restores the maximum size characteristic to the species.

B

back reef The inner part of a **barrier reef** (Fig. 14.18) or an **atoll** (Fig. 14.23).

bacteria (sing. **bacterium**) **Prokaryotic,** unicellular microorganisms in the domain *Bacteria.*

bacteriophages **Viruses** that infect **bacteria** (Fig. 5.1).

baleen The filtering plates that hang from the upper jaws of **baleen whales.**

baleen whales The filter-feeding whales.

bar-built estuary An **estuary** that is formed when a **barrier island** or *sand bar* separates a section of the coast where fresh water enters (Fig. 12.1).

barnacles **Crustaceans** that live attached to surfaces and are typically enclosed by heavy **calcareous** plates (Fig. 7.31).

barophilic **Pressure**-loving. Applied to organisms or enzymes that grow or function best, or only, at high pressure.

barrier island A long and narrow island that is built by waves along the coast.

barrier reef A type of **coral reef** that develops at some distance from the coast (Fig. 14.18).

basalt The dark-colored rock that forms the sea floor, or oceanic **crust.**

bathyal zone The bottom between the **shelf break** and a depth of approximately 4,000 m (13,000 ft) (Fig. 10.12).

bathypelagic zone The **pelagic** environment from a depth of 1,000 m (3,000 ft) to 4,000 m (13,000 ft) (Fig. 10.12).

beard worms (pogonophorans) Tube-dwelling **annelids** that lack a digestive system (Fig. 7.18).

benthos Organisms that live on the bottom (Fig. 10.11).

big bang theory The theory that a cosmic explosion produced clouds of dust and gas from which the earth and solar system originated.

bilateral symmetry The arrangement of body parts in such a way that there are only two identical halves, with different *anterior* and *posterior* ends and **dorsal** and **ventral** surfaces (Fig. 7.13). Compare **radial symmetry.**

binomial nomenclature A system of naming species using two names, the first of which refers to the **genus.**

biodegradable Able to be broken down by bacteria or other organisms.

biogenous sediment Sediment that is made up of the skeletons and shells of marine organisms. Also see **calcareous** and **siliceous ooze.**

biological clock A repeated rhythm that is synchronized with time.

biological magnification The increased concentration of **non-biodegradable** chemicals in the higher levels of the **food chain.**

bioluminescence The production of light by living organisms.

biomass The total mass of living organisms.

biotic A living component of the environment. Compare **abiotic.**

bioturbator A member of the **infauna** that moves sediment while burrowing or feeding.

birds (class *Aves*) **Vertebrates** that have feathers and lay eggs with calcified shells on land.

bivalves (class *Bivalvia*) *Clams, mussels,* and other **molluscs** that possess a two-valved shell, filtering gills, and a shovel-like **foot.**

black corals (order *Antipatharia*) Colonial **anthozoans** that secrete a black protein skeleton.

black smoker A chimney-like accumulation of mineral deposits that is found at **hydrothermal vents** (Figs. 2.26 and 2.27).

blade The leaf-like portion of the **thallus** of a **seaweed.**

bleaching The expulsion of **zooxanthellae** by reef corals in response to stress.

bloom A sudden increase in the abundance of an **alga** or **phytoplankton.**

blowhole The nostrils, or nasal openings, of **cetaceans.**

blubber A thick layer of fat under the skin of many marine **mammals.**

bony fishes (*Osteichthyes*) Fishes with a skeleton made mostly of bone; they also have **opercula** and **fin rays.**

boring sponges **Sponges** that bore through **calcareous** skeletons and shells.

bottom layer See **deep layer.**

brachiopods See **lamp shells.**

bradychardia The slowing down of heart rate during diving in marine mammals.

breaching Leaping into the air by whales (Fig. 9.29).

brittle stars (class *Ophiuroidea*) **Echinoderms** with five flexible arms that radiate from a conspicuous central disk and **tube feet** that are used in feeding.

brown algae (phylum *Heterokontophyta,* class *Phaeophyta*) **Seaweeds** with a predominance of yellow and brown pigments.

bryozoans (phylum *Ectoprocta* or *Bryozoa*) Small, colonial, **encrusting invertebrates** with delicate, often lace-like skeletons (Fig. 7.42).

budding A type of **asexual reproduction** by which a separate, new individual is produced from a small outgrowth, or *bud.*

by-catch Non-target catch that is taken while fishing for other species.

byssal threads Strong fibers secreted by mussels for attachment.

C

calcareous Made of **calcium carbonate.**

calcareous green algae **Green algae** that deposit **calcium carbonate** in their **thallus.**

calcareous ooze A type of **biogenous sediment** that is made of the **calcium carbonate** shells and skeletons of marine organisms.

calcium carbonate ($CaCO_3$) A mineral that is the major component of the shell, skeleton, and other parts of many organisms.

capsid The outer protein coat of **viruses.**

carapace (1) The shield-like structure that covers the anterior portion of some **crustaceans.** (2) The shell of *sea turtles.*

carbohydrate An **organic compound** that consists of chains or rings of **carbon** with **hydrogen** and **oxygen** attached to them.

carbon (C) An **element** that is an essential constituent of all **organic compounds.**

carbon cycle The cyclic conversion of **carbon** between **carbon dioxide** and various **organic compounds** (Fig. 10.20).

carbon dating A procedure used to determine the age of recent fossils.

carbon dioxide (CO_2) A colorless gas that is required in the process of **photosynthesis.**

carbon fixation The conversion of inorganic **carbon** (CO_2) into energy-rich organic carbon, usually by **photosynthesis.**

carnivore An animal that eats other animals. A *top carnivore* is one that feeds at the top of the **food chain.** Also see **predation.** Also used for the order *Carnivora,* **mammals** with teeth that are adapted to eat other animals. The marine members of this group are the *sea otter* and the *polar bear.*

carotenoid One of a group of yellow, orange, and red plant pigments.

carposporophyte A **diploid** generation found in the **red algae.** It produces non-motile *carpospores.*

carrageenan A **phycocolloid** extracted from **red algae** that is widely used in food processing.

carrying capacity The maximum population size that can be sustained by the available resources in a given environment.

cartilaginous fishes (*Chondrichthyes*) Fishes with a skeleton made of *cartilage: sharks, rays, skates,* and *ratfishes* (or *chimaeras*).

catadromous Freshwater fishes that migrate to sea to breed. Compare **anadromous.**

caudal fin The posterior, or tail, fin of fishes.

cellulose A complex **carbohydrate** that is the main component of fibers and other support structures in plants.

central nervous system The *brain* (or a similar aggregation of **nerve cells**) and one or more **nerve cords.**

central rift valley A depression in the **mid-ocean ridge** (Fig. 2.25).

cephalopods (class *Cephalopoda*) *Octopuses, squids,* and other **molluscs** that possess a **foot** modified into arms that surround the head.

cephalothorax The anterior portion of the body of many **arthropods,** which consists of the head fused with other body segments.

cetaceans (order *Cetacea*) Marine **mammals** with anterior flippers, no posterior limbs, and a **dorsal** fin: *whales, dolphins,* and *porpoises.*

CFCs See **chlorofluorocarbons.**

chaetognaths See **arrow worms.**

chemosynthetic (*chemoautotrophic*) **prokaryotes** **Autotrophic bacteria** (such as the *sulfur bacteria*) and **archaea** that use **energy** by releasing it from particular chemical compounds (Table 5.1).

chitin A complex derivative of **carbohydrates** that is the main component of the skeleton of many animals.

chitons (class *Polyplacophora*) **Molluscs** that have a shell divided into eight overlapping plates (Fig. 7.28).

chloride cells Cells in the **gills** of fishes that are involved in the excretion of excess salts.

chlorinated hydrocarbons A group of **non-biodegradable,** synthetic chemicals. Some are toxic and become pollutants.

chlorofluorocarbons (CFCs) Chemicals, used in sprays, air conditioners, and other products, that affect the **ozone layer.**

chlorophyll A green **photosynthetic pigment.**

chloroplast The **organelle** where **photosynthesis** takes place (Fig. 4.8*b*).

choanocyte See **collar cell.**

chordates (phylum *Chordata*) Animals that display a hollow **dorsal nerve cord, gill slits,** and a **notochord.** Includes the **protochordates** and the **vertebrates.**

chromatophore A skin cell that contains pigment.

chromosome The cell structure where **DNA** is located.

ciguatera A type of food poisoning contracted from eating certain tropical fishes. It results from a toxin produced by a **dinoflagellate.**

ciliary comb One of eight bands of **cilia** fused at the base that is found in **comb jellies.**

ciliates (phylum *Ciliophora*) A group of **protozoans** that have **cilia.**

cilium (pl. **cilia**) A short, hair-like **flagellum** that is found in large numbers and used in movement, for pushing food particles, and in other functions.

clasper A copulatory organ along the inner edge of each **pelvic fin** in male sharks and other **cartilaginous fishes** (Fig. 8.26).

cleaning associations A **symbiotic** association in which a smaller partner regularly removes parasites from fishes.

climax community The final stage in an **ecological succession.**

cloaca The common opening for the intestine and the excretory and reproductive systems of **cartilaginous fishes** and other animals.

clone A series of genetically identical cells or individuals that have developed from a single cell or individual.

cnidarians (phylum *Cnidaria*) **Invertebrates** with **nematocysts** and **radial symmetry.**

cnidocyte A cell that contains a **nematocyst** (Fig. 7.9).

coastal management The use of coastal resources with the intention of preserving them.

coastal plain estuary See **drowned river valley estuary.**

coccolithophorids (phylum *Heterokontophyta*, class *Haptophyta*) Unicellular, **eukaryotic** members of the **phytoplankton** that have calcareous, button-like structures, or *coccoliths* (Fig. 5.10).

coelacanths A group of lobed-fin fossil fishes. *Latimeria* was first discovered alive in 1952 (see figures on p. 171).

coelom The body cavity found in structurally complex animals (Fig. 7.16*c*).

coelomic fluid The fluid that fills the **coelom** of **echinoderms** and other **invertebrates.**

coevolution The process in which one **species** evolves in response to another.

collar cell (choanocyte) A flagellated, food-trapping cell of **sponges.**

colloblast Sticky cell used for the capture of small prey in **comb jellies.**

comb jellies (phylum *Ctenophora*) The **invertebrates** with a gelatinous body, **radial symmetry,** and eight rows of **ciliary combs** (Fig. 7.12).

commensalism The type of **symbiosis** in which one species obtains shelter, food, or other benefits without affecting the other, or *host*.

community The **populations** that live and interact in an area.

competition The interaction that results when a resource is in short supply and one organism uses the resource at the expense of another.

competitive exclusion The elimination of one species by another as a result of **competition.**

compound eye An eye typical of **arthropods** that consists of numerous light-sensitive units.

conditioning A form of learning in which a behavior is associated with a reward such as food.

constant proportions, rule of A principle that states that the relative amounts of ions in seawater are always the same.

consumer A **heterotroph.** A *primary consumer* feeds directly on a **primary producer,** whereas a *secondary consumer* feeds on a primary consumer.

continental drift The movement of continental masses on the surface of the earth.

continental margin The edge of a continent; the zone between a continent and the deep-sea floor (Fig. 2.19). Also see **active** and **passive continental margins.**

continental rise The gently sloping area at the base of the **continental slope** (Fig. 2.19).

continental shelf The shallow, gently sloping section of the **continental margin** that extends from the shore to the point where the slope gets steeper (Fig. 2.19).

continental slope The steeper, seaward section of the **continental margin** (Fig. 2.19).

convection The movement that results when heat is transferred in a fluid, such as the heat-driven motion observed in the earth's mantle.

convergent evolution **Evolution** in which two different species evolve similar structures because of similar lifestyles.

copepods Small, mostly planktonic **crustaceans** (Fig. 7.30).

copulation The sexual union undertaken to transfer **gametes.**

coral knoll (pinnacle) A column of coral within the **lagoon** of an **atoll** (Fig. 14.23).

coralline algae **Red algae** that deposit **calcium carbonate** in their **thallus.**

coralline sponges See **sclerosponges.**

coral reef A massive deposit of **calcium carbonate** by colonial **stony corals** and other organisms.

coral rubble Coral fragments.

cordgrasses Salt-tolerant grasses, species of *Spartina,* that inhabit **salt marshes** (Fig. 12.7).

core The innermost layer of the earth (Fig. 2.3).

Coriolis effect The tendency of objects moving large distances on the earth's surface to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere (Fig. 3.16).

counterillumination The emission of light by **midwater** animals to match the background light (Fig. 16.15).

countershading A color pattern that results in a dark back and a light belly; most common in **epipelagic fishes** (Fig. 15.18).

courtship behavior Behavior related to attracting the opposite sex and mating.

crinoids (class *Crinoidea*) **Echinoderms** with a small, cup-shaped body and feathery arms: the *sea lilies* and *feather stars* (Fig. 7.50).

crown-of-thorns sea star (*Acanthaster planci*) A *predator* of reef corals (Fig. 14.31).

crust The outermost layer of the earth (Fig. 2.3).

crustaceans (subphylum *Crustacea*) **Arthropods** that have two pairs of **antennae** and an **exoskeleton** hardened by **calcium carbonate.**

cryptic coloration A color pattern that allows an organism to blend with the surroundings.

Cryptophytes (phylum *Cryptophyta*) Unicellular, **eukaryotic** members of the **phytoplankton** that have two flagella and no skeleton.

crystal A solid that consists of a regular pattern of molecules.

crystalline style An **enzyme**-releasing rod in the stomach of **bivalves** (Fig. 7.23*b*).

ctenophores See **comb jellies.**

current A horizontal movement of water.

cyanobacteria A group of generally **photosynthetic** bacteria. Formerly known as *blue-green algae.*

cytoskeleton A complex framework inside cells made of protein fibers.

D

decapods **Crustaceans** with five pairs of walking legs and a well-developed **carapace.** The group includes the *shrimps, lobsters, hermit crabs,* and *crabs.*

decomposers Organisms such as *decay* **bacteria** and **archaea** that break down dead organic matter into smaller molecules.

deduction Reasoning from general principles to specific conclusions.

deep (bottom) layer The deepest and coldest of the three layers of the ocean (Fig. 3.24).

deep scattering layer (DSL) A sound-reflecting layer made up of many types of organisms that migrate daily from the **mesopelagic zone** to the **epipelagic zone.**

deep sea The dark waters below the **mesopelagic zone** (Fig. 10.12).

deep-sea fan A fan-like accumulation of sediment at the base of a **submarine canyon.**

delayed implantation The delay in the attachment of the early **embryo** to the womb in **pinnipeds** and some other **mammals** in order to time birth with favorable conditions.

demersal fish A bottom-dwelling fish.

density The weight (or more correctly the *mass*) of a given volume of a substance.

deposit feeder An animal that feeds on organic matter that settles on the bottom (Fig. 7.3). Compare **suspension feeder.**

desalination The conversion of seawater into fresh water.

detritus Particles of dead organic matter.

diatomaceous ooze A **biogenous sediment** that consists mostly of the **siliceous frustules** of **diatoms.** It is known as *diatomaceous earth* when found inland.

diatoms (phylum *Heterokontophyta,* class *Bacillariophyta*) Unicellular and **eukaryotic autotrophs** with a **siliceous frustule;** mostly **planktonic** (Figs. 5.6 and 15.3).

diffusion The movement of molecules from an area of high concentration to an area of low concentration.

digestive gland An **enzyme**-producing gland in several groups of **invertebrates** where digestion and absorption take place.

dinoflagellates (phylum *Dinoflagellata*) Unicellular, **eukaryotic,** mostly **autotrophic protists** with two unequal **flagella** (Fig. 5.8).

dioxins A group of toxic **chlorinated hydrocarbon** pollutants.

diploid (2*n*) cell A cell, such as a body cell, that contains two similar sets of **chromosomes,** one from each parent. Compare **haploid.**

dispersal The manner in which organisms get from place to place.

disruptive coloration A color pattern that helps break the outline of an organism.

dissociation The breaking up of a salt molecule into **ions** when placed in water or other solvents (Fig. 3.5).

dissolved organic matter (DOM) Organic matter that is dissolved in water rather than being in particles.

diurnal tide A tidal pattern with a high and a low **tide** each day (Fig. 3.34*c*).

diversity The total number of species inhabiting a particular environment.

DNA (deoxyribonucleic acid) Nucleic acids that contain the inherited genetic code that specifies the structure and function of an organism.

domestic sewage Wastewater from homes and non-industrial buildings. Compare **industrial sewage.**

domoic acid Toxin produced by some planktonic **diatoms.**

dorsal The upper or back surface of an animal with **bilateral symmetry** (Fig. 7.13*b*).

downwelling The sinking of surface water that is denser than underlying water layers.

drag Resistance to movement through water or any other medium.

drift net A fishing net that is allowed to drift for a long time before it is pulled on board.

drowned river valley (coastal plain) estuary An **estuary** that is formed when sea level rose at the end of the last glacial age.

E

ear stone (otolith) A calcareous body in the **inner ear** of fishes and other **vertebrates** that is used in the maintenance of equilibrium. Also see **statocyst.**

echinoderms (phylum *Echinodermata*) **Invertebrates** with five-way **radial symmetry** and a **water vascular system.**

echiurans (phylum *Echiura*) Burrowing **invertebrates** that have an unsegmented body and a non-retractable **proboscis** (Fig. 13.9).

echolocation The ability of some animals to sense their surroundings by analyzing the reflection of sound waves, or clicks, they emit.

ecological niche The full range of ecological characteristics of a species, such as its feeding habits, specific **habitat,** and reproductive strategy.

ecological succession The regular replacement of **species** by others in a given area.

ecology The study of the interactions between organisms and their environment.

ecosystem A **community** or communities plus the physical environment, interacting in a large, more or less self-contained area.

ectoprocts See **bryozoans.**

ectotherm An organism that loses metabolic heat to the environment without it affecting its body temperature. Compare **endotherm.**

Ekman spiral The spiral change in the movement of water in the **water column** when the water is pushed by wind (Fig. 3.19). The *Ekman layer* is that part of the water column affected by wind; *Ekman transport* is the net water movement 90° from the wind direction.

element A substance that consists of **atoms** of the same kind and that cannot be decomposed by ordinary chemical means.

El Niño–Southern Oscillation (ENSO) Large-scale changes in atmospheric and ocean current patterns in which, among other things, warm surface water in the Pacific Ocean moves further to the east than normal. *El Niño* refers specifically to the warming of the surface water in the Eastern Pacific. Compare **La Niña.**

embryo The early developmental stage that, through *embryological development,* ultimately becomes an adult individual.

encrusting Describing an organism that grows as a crust over rocks and other hard surfaces.

endangered species A species that is in immediate danger of **extermination.**

endolithic alga An alga that burrows into **calcareous** rocks or corals.

endophyte A photosynthetic organism that lives within the cells or tissues of algae or plants. Compare **epiphyte.**

endoplasmic reticulum An extensive system of folded membranes present in most **eukaryotic cells** (Fig. 4.8).

endoskeleton A skeleton under the external surface of an animal. Compare **exoskeleton.**

endotherm An organism that retains some metabolic heat, which raises its body temperature. Compare **ectotherm.**

energy The ability to do work.

enzyme A **protein** that speeds up a specific chemical reaction.

epifauna Animals that live on the surface of the **substrate.** Compare **infauna.**

epipelagic zone The **pelagic** environment from the surface to a depth of 100 to 200 m (350 to 650 ft) (Fig. 10.12).

epiphyte A photosynthetic organism that lives on algae or plants. Compare **endophyte.**

equatorial currents Major ocean currents that move parallel to the Equator (Fig. 3.20).

erythrocyte (red blood cell) A specialized type of blood cell that carries **hemoglobin** in **vertebrates.**

estuary A semi-enclosed area where fresh water and seawater meet and mix.

eukaryote An organism that consists of one or more **eukaryotic cells.**

eukaryotic cell A cell that contains a **nucleus** and other **organelles** (Fig. 4.8). Compare **prokaryotic cell.**

euryhaline An organism that can tolerate a wide range of salinities. Compare **stenohaline.**

eutrophication Accelerated growth of algae in response to increased nutrient input.

evaporation The escape of molecules from the liquid phase into the gaseous phase, or vapor.

evaporative cooling The lower speed and hence lower temperature of molecules remaining in the liquid phase after **evaporation** of the fastest molecules.

evisceration The expulsion of internal organs in **sea cucumbers.**

evolution A change in the genetic makeup of a species, usually as a result of **natural selection** favoring some individual characteristics over others.

evolutionary adaptation The genetic adaptation of a population to its environment through **evolution.**

exclusive economic zone (EEZ) A zone 200 nautical miles (370 km) wide along the coast where nations have exclusive rights to any resource. It was initiated by the *United Nations Convention on the Law of the Sea (UNCLOS).*

exoskeleton A skeleton that forms the external surface of an animal, as in **arthropods.** Compare **endoskeleton.**

experiment An artificially created situation that is used to test a **hypothesis.** In a *controlled experiment,* additional variables that might affect the experiment are prevented from doing so.

extermination (extirpation) The **extinction** of a species that is caused by humans.

extinction The disappearance of a species.

extracellular digestion Digestion that takes place outside cells, usually in a gut, or digestive cavity. Compare **intracellular digestion.**

F

fault A crack in the earth's crust usually formed when two pieces of crust are moving past each other.

feather stars See **crinoids.**

fertilization The union of **gametes.** It can be *external* and take place in the water or *internal* and take place within the body.

fetch The span of the sea surface over which the wind blows to form wind-driven **waves** (Fig. 3.28).

filter feeder A **suspension feeder** that actively filters food particles (Fig. 7.3).

fin ray Each of the bony spines in the fins of **bony fishes.**

fish meal A fish-protein supplement used in animal feeds.

fish protein concentrate (**FPC** or **fish flour**) A fish protein supplement for human consumption.

fission A type of **asexual reproduction** that results when one individual splits into two individuals.

fjord An **estuary** that is formed in a deep valley created by a retreating glacier (Fig. 12.2).

flagellum A long, whip-like **organelle** that is usually involved in locomotion.

flatworms (phylum *Platyhelminthes*) **Invertebrates** that are dorsoventrally flattened and have an incomplete digestive tract, true **organs,** and **organ systems.**

flowering plants (**angiosperms;** division *Anthophyta*) Plants that have flowers, seeds, and true leaves, stems, and roots.

fluke The fin-like tail of **cetaceans.**

flukes A group of parasitic **flatworms.**

food chain The steps of transfer of **energy** from **primary producers** through **consumers.**

food web All of the interconnecting feeding relationships in a **community.**

foot The muscular locomotory structure of **molluscs.**

foraminiferan ooze A **biogenous sediment** that consists mostly of the **calcareous** shells of **foraminiferans.**

foraminiferans (forams) (phylum *Granuloreticulosa*) **Protozoans** with a **calcareous** shell, or *test,* and **pseudopodia** (Fig. 5.11).

fore reef The outer part of a **barrier reef** (Fig. 14.18) or an **atoll** (Fig. 14.23).

fouling organisms Organisms that live attached to submerged surfaces such as boats and pilings.

fringing reef A **coral reef** that develops as a narrow band close to a shore (Fig. 14.15).

frustule The **siliceous,** box-like cell wall of **diatoms.**

fucoxanthin The yellow to golden brown **photosynthetic pigment** of **brown algae.**

fungi (sing. **fungus**) Plant-like but non-photosynthetic organisms; members of the kingdom *Fungi.*

funnel See **siphon.**

G

gamete A **haploid** reproductive cell that develops into a new individual after its union with another gamete.

gametophyte The **haploid,** gamete-producing generation in many **seaweeds.** Compare **sporophyte.**

gas exchange The movement of **oxygen** and other gases between the atmosphere and the ocean, or between the water or atmosphere and living organisms, in which case it is often called **respiratory exchange.**

gastropods (class *Gastropoda*) Snails and other **molluscs** that typically possess a coiled **dorsal** shell and a **ventral** creeping **foot.**

genetic engineering The artificial alteration of the genetic information of an individual.

genital slit The genital opening of **cetaceans.**

genome The complete genetic information of an organism.

genus A group of similar **species.**

gestation The length of time between **fertilization** and birth in **mammals.**

gill Thin-walled extensions of the body that are used in **gas exchange.**

gill arch A supporting structure of fish **gills.**

gill cover See **operculum.**

gill filament The thin projection of a fish **gill** where **gas exchange** takes place (Fig. 8.17*b*).

gill raker Each of the projections along the inner surface of fish **gills** (Fig. 8.17*b*).

gill slit (pharyngeal slit) One of several pairs of openings along the **pharynx** in **chordates** (Figs. 7.51*b* and 7.54).

glass sponges Deep-water **sponges** with a skeleton of fused **silica spicules.**

global distillation **Evaporation** and condensation of substances on a global scale, leading to the net transport of certain pollutants to the poles.

global warming A long-term increase in the global average temperature. **Anthropogenic** (human-caused) global warming results from an intensified greenhouse effect due to human emissions of greenhouse gases.

glucose A **simple sugar** that plays an important role in the **metabolism** of most organisms.

Golgi apparatus An arrangement of sacs and membranes in many **eukaryotic cells** that is involved in collecting and transporting molecules (Fig. 4.8).

gonad An organ that contains the *germ tissue* that produces the **gametes:** *ovary* and *testis.*

Gondwana One of two large continents, the southern one, that formed when the supercontinent **Pangaea** broke up about 180 million years ago (Fig. 2.16*b*). Also see **Laurasia.**

gorgonians (order *Gorgonacea*) Colonial **anthozoans** that secrete a skeleton made of protein (Fig. 7.11).

granite The light-colored rock that forms most of the continental **crust.**

grazer An organism that feeds primarily on plants.

great ocean conveyor A global circulation pattern in which water cycles throughout the ocean basins (Fig. 3.25).

great whales Large whales: the sperm and the **baleen whales.**

green algae (phylum *Chlorophyta*) **Seaweeds** in which **chlorophyll** is not masked by other pigments.

greenhouse effect The retention of heat in the lower atmosphere due to the presence of **carbon dioxide,** water vapor, and other greenhouse gases that allow solar light energy to penetrate to the earth's surface but block the transmission of heat energy back into space.

guano The accumulation of the excrement of seabirds.

guyot A flat-topped **seamount.**

gyre A large, nearly circular system of wind-driven surface currents that center around latitude 30° in both hemispheres (Fig. 3.20).

H

habitat The natural environment where an organism lives.

habitat restoration The recovery of stressed or destroyed habitats.

hadal zone The bottom below 6,000 m (20,000 ft) (Fig. 10.12).

hadopelagic (hadal pelagic) zone The **pelagic** environment below 6,000 m (20,000 ft) (Fig. 10.12).

halophyte A salt-tolerant terrestrial plant.

haploid (*n*, or 1*n*) cell A cell, such as a **gamete,** that contains only half the normal number of chromosomes found in **diploid,** or body, **cells.**

harem A large group of females herded by a large male **pinniped** for the purpose of mating; harems also occur in some fishes.

harmful algal blooms Unusual population explosions, or **blooms,** of **phytoplankton** that are detrimental to humans.

heart urchins Burrowing **sea urchins** with a flattened test and short spines (Fig. 13.7).

heat capacity The amount of heat that must be added to a substance to raise its temperature by a given amount, which reflects the substance's ability to store heat.

heavy metals A group of toxic metals: *mercury, lead,* and others.

hemichordates (phylum *Hemichordata*) **Invertebrates** with a **dorsal nerve cord** and **gill slits.** Includes the *acorn worms,* or *enteropneusts.*

hemoglobin A blood **protein** that transports **oxygen** in many animals.

herbivore An animal that eats plants.

heredity The transmission of genetic characteristics from one generation to the next.

hermaphrodite An organism that has both male and female **gonads.** In *simultaneous hermaphroditism* sperm and eggs can be produced at the same time; in *sex reversal,* or *sequential hermaphroditism,* an individual begins life as a male but changes into a female (*protandry*) or as a female but changes into a male (*protogyny*).

hermatypic coral Corals that build **coral reefs.**

heterotroph An organism that obtains **energy** from organic matter.

holdfast The root-like portion of the **thallus** of a **seaweed.**

holoplankton Organisms that spend their entire lives in the **plankton.** Compare **meroplankton.**

homeotherm An organism that is able to keep its body temperature more or less constant regardless of the temperature of the environment. Compare **poikilotherm.**

homing The ability of an animal to find its home area.

hormone A substance that acts as a chemical messenger in an organism.

horseshoe crabs (class *Merostomata*) **Arthropods** with a large, horseshoe-shaped **carapace** (Fig. 7.40).

hydrogen An element that is one of the constituents of water, organic matter, and many other chemicals. Hydrogen gas (H_2) is composed of two hydrogen **atoms.**

hydrogen bond Weak bonds between water **molecules** that result from an attraction between the **hydrogen** atoms of one molecule and the **oxygen** atoms of adjacent molecules (Fig. 3.1).

hydrogen sulfide (H_2S) The gas that is produced in **anoxic** sediments.

hydrostatic skeleton A system that uses water pressure against the body wall to maintain body shape and aid in locomotion.

hydrothermal vent A deep-sea hot spring where heated seawater forces its way up through the **crust** (Figs. 2.26 and 2.27).

hydrozoans (class *Hydrozoa*) **Cnidarians** whose life cycle typically includes a **polyp,** which is often colonial, and a **medusa.**

hypothesis A statement that might be true.

hypoxic Sharp reduction of water oxygen as in *hypoxic* or *dead zones.* Compare **anoxic.**

I

ice age A period of time when significant amounts of ice form on the continents, inducing a fall in sea level.

Indo-West Pacific region The tropical Indian and western and central Pacific oceans.

inducible defenses Defense mechanisms that an organism uses only in response to predators.

induction Reasoning from specific observations to a general conclusion.

industrial sewage Wastewater from industries. Compare **domestic sewage.**

infauna Animals that burrow in the **substrate.** Compare **epifauna.**

ink sac A gland found in some **cephalopods** that secretes a dark fluid used to discourage predators.

inner ear A paired, sound-sensitive organ in **vertebrates.**

insects (class *Insecta*) **Arthropods** with three pairs of legs and one pair of **antennae.** Few are marine, an exception being the *water strider* (Fig. 15.17).

interglacial period A geological period between **ice ages** when, as at present, the earth's climate is relatively warm.

intermediate layer Of the three main layers of the ocean, the one below the **surface,** or **mixed,** layer. It includes the main **thermocline** (Fig. 3.24).

International Whaling Commission (IWC) An agency that regulates *whaling* around the world.

interspecific competition **Competition** among members of different species. Compare **intraspecific competition.**

interstitial fauna Animals living between sediment particles. Also see **meiofauna.**

interstitial water The water contained between sediment particles.

intertidal (littoral) zone The area between the highest and lowest tide (Fig. 10.12).

intracellular digestion Digestion that takes place within cells, usually those lining the gut or digestive tract. Compare **extracellular digestion.**

intraspecific competition **Competition** among members of the same species. Compare **interspecific competition.**

invasive species (introduced, alien, or **exotic species)** A species introduced into a new environment by humans. Compare **native species.**

invertebrates Animals that lack a backbone.

ion An atom or a group of atoms that is electrically charged.

iridophore A **chromatophore** with light-reflecting **crystals.**

island arc A curved chain of volcanic islands that form along a **trench.**

isopods Small, dorsoventrally flattened **crustaceans** such as the *sea louse* (Fig. 7.33).

isotopes Different atomic forms of an **element.**

J

jawless fishes (*Agnatha*) Fishes that lack jaws and paired fins: *hagfishes* (or *slime eels*) and *lampreys* (Fig. 8.2).

K

kelp **Brown algae** characterized by their large size and complexity. Some, like the giant kelp, form dense *kelp beds* or *kelp forests.*

keystone predator A predatory species whose effects on its community are proportionately much greater than its abundance.

krill (euphausiids) Planktonic **crustaceans** that are an important food of whales and other animals (Fig. 17.12).

L

lactic acid Harmful product of **anaerobic respiration** in muscles.

lagoon A shallow, sheltered body of water separated from the open sea by **coral reefs,** *sand bars,* and/or **barrier islands** (Figs. 14.18 and 14.23).

lamella (pl. **lamellae**) Each of the many thin plates that make up the **gill filaments** of fish **gills** (Fig. 8.17*c*).

lamp shells (brachiopods; phylum *Brachiopoda*) **Invertebrates** that have a lophophore and a shell that consists of two **valves.**

lancelets (subphylum *Cephalochordata*) **Chordates** with the three basic chordate characteristics but lacking a backbone (Fig. 7.53).

La Niña Large-scale changes in atmospheric and ocean current patterns in which, among other things, warm surface water in the Pacific Ocean moves further to the west than normal. Compare **El Niño–Southern Oscillation.**

larva Immature stage of an animal that looks different from the adult.

larvaceans (appendicularians; class *Larvacea*) **Tunicates** that retain the body of a **tadpole larva** throughout life (Fig. 15.9).

latent heat of evaporation The amount of heat **energy** that is needed to evaporate a substance, that is, to change it from a liquid to a gas.

latent heat of melting The amount of heat **energy** needed to melt a substance, that is, to change it from a solid to a liquid.

lateral line A system of canals and sensory cells on the sides of fishes that helps them detect vibrations in the water (Fig. 8.19).

Laurasia One of the two large continents, the northern one, that formed when the supercontinent **Pangaea** broke up about 180 million years ago (Fig. 2.16*b*). Also see **Gondwana.**

leeches (class *Hirudinea*) **Segmented worms** that are specialized predators and parasites.

leptocephalous larva The leaf-shaped larva of freshwater eels and other fishes.

lichen The organism that results from the **symbiosis** of a **fungus** and an **autotroph** such as a **green alga.** (Fig. 5.14).

limiting resource An essential factor whose short supply limits the growth of a **population.**

lipid A group of **organic molecules** that are often used by organisms in the long-term storage of **energy,** waterproofing, buoyancy, and insulation.

lithogenous sediment Sediment that is derived from the breakdown, or **weathering,** of rocks. Also see **red clay.**

lithosphere The **crust** and the top part of the mantle that covers the earth's surface. It is broken into separate *lithospheric plates* (Fig. 2.10).

littoral zone See **intertidal zone.**

lophophore A feeding structure that consists of ciliated tentacles.

loriciferans (phylum *Loricifera*) Tiny invertebrates that live among sediment particles and have a body enclosed by six plates.

lysogenic viruses **Viruses** that reproduce when their **nucleic acid** becomes part of the **genome** of the host cells.

M

macroplankton The component of the plankton that consists of large organisms 2 to 20 cm in size (Fig. 15.2).

madreporite A porous plate that connects the **water vascular system** of **echinoderms** to the exterior.

magnetic anomalies Magnetic bands in the sea floor that run parallel to the **mid-ocean ridge** (Fig. 2.8).

main thermocline See **thermocline.**

male parasitism The permanent attachment of a male to a female in some deep-sea fishes (Fig. 16.21).

mammals (class *Mammalia*) **Vertebrates** that have hair and **mammary glands.**

mammary glands The milk-secreting glands of **mammals.**

mangroves Shrubs and trees that live along the seashore in tropical and subtropical regions and tolerate inundation by seawater (Fig. 6.14).

mantle (1) The semi-liquid region between the **crust** and **core** of the earth (Fig. 2.3). (2) The outer layer of tissue that secretes the shell of **molluscs** (Figs. 7.20, 7.25, and 7.27).

mantle cavity The space lined by the **mantle** of **molluscs** (Figs. 7.20, 7.25, and 7.27).

mariculture The culture of marine organisms. In *open mariculture* (or *semiculture*), organisms are cultured in natural environments; in *closed mariculture* (or *intensive mariculture*), organisms are cultured in a controlled environment.

marine archaeology The discovery, salvage, and interpretation of material remains of humankind's past that have been preserved in the sea.

marine natural products Chemical compounds that are obtained from marine organisms.

marine snow Large, fluffy **detritus** particles that are found in the **water column.**

maritime culture A human culture with a very close relationship with the sea.

maxillipeds The food-sorting appendages of some **crustaceans.**

maximum sustainable yield The maximum catch of a **stock** that can be harvested year after year without diminishing the stock.

medusa The bell-shaped, free-swimming stage of **cnidarians.**

megaplankton The component of the plankton that consists of very large organisms over 20 cm in size (Fig. 15.2).

meiofauna Microscopic animals that live on the bottom; often used as a synonym of **interstitial fauna.**

meiosis Cell division that results in the formation of **gametes.**

melon A fatty structure on the forehead of some **cetaceans** that is used to direct sound waves emitted during **echolocation** (Fig. 9.27).

meroplankton Planktonic organisms that spend only part of their life in the **plankton.** Compare **holoplankton.**

mesenterial filament Any of the long, thin tubes attached to the gut of corals and other **cnidarians** that are involved in digestion and absorption.

mesoglea The layer between the *epidermis* and *gastrodermis* in **cnidarians** (Figs. 7.6 and 7.9).

mesopelagic zone The **pelagic** environment from a depth of approximately 100 to 200 m (350 to 650 ft) to 1,000 m (3,000 ft) (Fig. 10.12).

mesoplankton The component of the **plankton** that consists of organisms 0.2 to 2 mm in size (Fig. 15.2).

metabolism All the chemical reactions that take place in an organism.

metamorphosis A marked change in form during embryological development.

microbial loop A component of **pelagic food webs** in which **dissolved organic matter** is cycled through the **picoplankton** and **nanoplankton** back into the main part of the food web (Fig. 15.25).

microfossils The microscopic shells and other remains of marine organisms that make up **biogenous sediments.**

microplankton The component of the **plankton** that consists of organisms 20 to 200 microns (µm) (0.02 to 0.2 mm) in size (Fig. 15.2).

mid-ocean ridge The continuous chain of volcanic submarine mountains that extends around the earth. It includes the *Mid-Atlantic Ridge* and *East Pacific Rise* (Figs. 2.5 and 2.9).

midwater Pertaining to the **mesopelagic zone.**

migration The regular movement of one organism from one place to another.

mitochondrion The **organelle** in which **respiration** takes place in **eukaryotes** (Fig. 4.8).

mitosis The cell division in which a cell divides into two daughter cells that are identical to the original cell.

mixed layer See **surface layer.**

mixed semidiurnal tide A tidal pattern with two successive high **tides** of different heights each day (Fig. 3.34*b*).

molecule A combination of two or more **atoms.**

molluscs (phylum *Mollusca*) **Invertebrates** with a soft, unsegmented body, a muscular **foot,** and, with some exceptions, a **calcareous** shell.

molt The **exoskeleton** that is shed during the *molting* process.

monsoon Winds in the northern Indian Ocean that blow from the southwest in summer and from the northeast in winter.

mudflat A muddy bottom that is exposed at low tide.

mutualism The type of **symbiosis** in which both partners benefit from the relationship.

myoglobin A type of muscle protein that stores **oxygen** in **vertebrates.**

myomere Each of the bands of muscles along the sides of fishes.

N

nanoplankton The component of the **plankton** that consists of very small organisms 2 to 20 microns (µm) (0.002 to 0.2 mm) in size (Fig. 15.2); they are too small to catch in a standard plankton net.

native species A species that naturally occurs in a given area. Compare **invasive species.**

natural selection A mechanism of evolutionary change that results when individuals that are better *adapted* than others in meeting the challenges of the environment produce more offspring.

nauplius A planktonic **larva** of many crustaceans (Figs. 7.39 and 15.11*e*).

neap tides The **tides** with a small **tidal range.** They occur around the times when the moon is in quarter. Compare **spring tides.**

negative estuaries **Estuaries** where loss of fresh water through evaporation is higher than freshwater input from rivers.

nekton Organisms that swim strongly enough to move against the current (Fig. 10.11).

nematocyst The stinging structure of **cnidarians.**

nematodes (roundworms; phylum *Nematoda*) **Invertebrates** with a cylindrical body, a conspicuous body cavity, and a complete digestive tract.

nemerteans See **ribbon worms.**

neritic zone The **pelagic** environment above the **continental shelf** (Fig. 10.12).

nerve cell A cell specialized to originate or transmit nerve impulses.

nerve cord A long, compact bundle of **nerve cells** that is part of the **central nervous system.**

nerve net The network of interconnecting **nerve cells** in **cnidarians** and other **invertebrates.**

net plankton **Plankton** that can be caught in a standard plankton net.

neuston Organisms that live right at the sea surface but remain underwater. Compare **pleuston.**

niche See **ecological niche.**

nictitating membrane A thin layer of tissue that can be drawn across the eye in sharks and some other **vertebrates.**

nitrate (NO_3^{-1}) An important **nutrient** in the ocean.

nitrogen (N_2) An **element** that is one of the constituents of **proteins.** Nitrogen gas (N_2) is composed of two nitrogen **atoms.**

nitrogen cycle The cycling of **nitrogen** among various nitrogen compounds (Fig. 10.21).

nitrogen fixation The conversion of gaseous **nitrogen** (N_2) into nitrogen compounds that can be utilized by **autotrophs.** It is performed by *nitrogen fixers* (Table 5.1).

non-biodegradable Unable to be broken down by bacteria or other organisms.

non-renewable resource A resource that is not naturally replaced.

notochord A flexible rod that lies below the **nerve cord** of **chordates.**

nucleic acid **Organic molecules** that store and transmit genetic information. Also see **deoxyribonucleic acid, ribonucleic acid.**

nucleus The **organelle** of **eukaryotic cells** that contains the **chromosomes** (Fig. 4.8).

nudibranchs (sea slugs) **Gastropods** that lack a shell and have exposed **gills.**

nutrient A raw material other than **carbon dioxide** and water that is needed by an **autotroph** to produce **organic** matter. Examples are **nitrate** and **phosphate.**

nutrient regeneration The release of nutrients from organic matter by **decomposers.**

O

ocean acidification Decrease of seawater pH as a result of increased **carbon dioxide.**

ocean thermal energy conversion (OTEC) A process for obtaining **energy** by exploiting depth differences in temperature (Fig. 17.21).

oceanic zone The **pelagic** environment beyond the **shelf break** (Fig. 10.12).

olfactory sacs Structures on both sides of the head of fishes that are sensitive to chemical stimuli.

operculum (1) The tough lid that closes the shell opening of many **gastropods** when the body is withdrawn. (2) The flap of bony plates that covers the **gills** of **bony fishes.**

organ A group of **tissues** specialized for one function.

organelle A membrane-bound, specialized structure within a cell (Fig. 4.8).

organic compound A **molecule** that contains **carbon, hydrogen,** and usually **oxygen.**

organization, level of The extent of specialization and organization of the cells of an organism. Organization may be at the *cellular, tissue,* or *organ* level.

osculum A large opening in many **sponges.**

osmoconformer An organism that allows its internal **salt** concentration to change with the **salinity** of the surrounding water.

osmoregulator An organism that controls its internal **salt** concentration.

osmosis The movement of water across a *selectively permeable* membrane, such as the cell membrane, which allows only certain molecules to pass through.

outwelling The export of **detritus** and other organic matter from estuaries to other ecosystems.

overturn The sinking of surface water that has become more dense than the water below (Fig. 3.23).

oviparous An animal that releases eggs.

ovoviviparous An animal that produces eggs that hatch inside the female immediately before birth.

ovulation The release of an egg from the ovary.

oxygen An **element** that is one of the constituents of water, organic matter, and many other chemicals. Oxygen gas (O_2), composed of two oxygen **atoms,** is needed for **respiration** and is produced by **photosynthesis.**

oxygen minimum zone A layer of water at a depth of approximately 500 m (1,600 ft) where **oxygen** is depleted (Fig. 16.18).

oyster reef A dense oyster bed present in some **estuaries** and other marine environments.

ozone layer Ozone (O_3) in the atmosphere that deflects ultraviolet radiation, which is harmful to life.

P

Pangaea The single large landmass, or supercontinent, that broke up to form today's continents (Fig. 2.16*a*).

Panthalassa The large ocean that surrounded the supercontinent **Pangaea** and that was the ancestor of the modern Pacific Ocean (Figs. 2.16*a* and 2.16*b*).

paralytic shellfish poisoning A condition caused when humans eat shellfish that have become contaminated with the toxin present in certain **dinoflagellates** that cause **red tides.**

parapodium A usually flat lateral extension present on each of the body segments of **polychaetes** (Fig. 7.16).

parasitism The type of **symbiosis** in which one partner, the *parasite,* derives benefit from the other, the *host.*

parthenogenesis Development of an egg into an embryo without fertilization by a sperm.

passive continental margin A **continental margin** that is located at the "trailing edge" of a continent and as a result shows little geological activity (Fig. 2.22). Compare **active continental margin.**

patchiness The grouping of organisms in clumps or patches.

PCBs See **polychlorinated biphenyls.**

peanut worms (**sipunculans;** phylum *Sipuncula*) Burrowing **invertebrates** with an unsegmented body and an anterior end that can be pulled into the body (Fig. 7.19).

pectoral fin Each of the pair of fins just behind the head of fishes (Fig. 8.8).

pedicellaria One of the minute, pincer-like organs of some **echinoderms** that help keep the body surface clean.

pelagic organisms Organisms that live in the **water column,** away from the bottom, including the **plankton** and **nekton** (Fig. 10.11).

pelvic fin Each of the second pair of **ventral** fins of fishes (Fig. 8.8).

pen The reduced, thin shell of squids.

perennial A plant that lives more than two successive years.

pharynx The anterior portion of the digestive tract of many animals. It is located directly behind the mouth cavity.

pheromone A chemical that organisms use to communicate with other members of their species.

phoronids (phylum *Phoronida*) Tube-dwelling, unsegmented **invertebrates** that possess a horseshoe-shaped or circular **lophophore.**

phosphate (PO_4^{-3}) A source of **phosphorus** important to marine **primary producers.**

phosphate cycle The cycling of **phosphorus** among various phosphorus compounds.

phosphorus (P) An **element** that is essential to life.

photic zone The surface layer where there is enough light for **photosynthesis** to occur. Also see **epipelagic zone.**

photophore (light organ) An organ that produces **bioluminescence.**

photosynthesis The chemical process involved in the transformation of solar energy into **glucose** (Fig. 4.4):

$$CO_2 + H_2O \xrightarrow{\text{sun energy}} \underset{\text{(glucose)}}{\text{organic matter}} + O_2$$

photosynthetic pigment A **molecule** such as **chlorophyll** that is responsible for capturing solar **energy** in **photosynthesis.**

phycobilins A group of **photosynthetic pigments** that includes *phycocyanin,* a bluish pigment in **cyanobacteria,** and *phycoerythrin,* a red pigment in **red algae.**

phycocolloid One of several **starch**-like chemicals found in some **seaweeds.** They are of significant commercial importance. Also see **agar, algin,** and **carrageenan.**

phycocyanin See **phycobilins.**

phycoerythrin See **phycobilins.**

phylogeny The evolutionary history of a **species** or other **taxon.**

phylum The **taxon** that represents a main division of a kingdom. The equivalent term *division* is used in the kingdom Plantae.

physiological adaptation Non-inherited adaptation to the environment in an individual.

phytoplankton The photosynthetic component of **plankton** consisting primarily of single-celled algae and bacteria. Compare **zooplankton.**

picoplankton The component of the **plankton** that consists of extremely small organisms, 0.2 to 2 microns (µm) (0.0002 to 0.002 mm) in size (Fig. 15.2); they are too small to catch in a standard plankton net.

pinacocyte The flat cells on the outer surface of **sponges.**

pinnipeds (order *Pinnipedia*) **Mammals** with paddle-shaped flippers: *seals, eared seals* (*sea lions* and *fur seals*), and the *walrus.*

placenta A membrane that connects the mammalian **embryo** with the mother's womb to provide nourishment.

planktivore An animal that feeds on **plankton.**

plankton Organisms that drift in the water (Fig. 10.11).

plants Members of the kingdom *Plantae,* which consists of photosynthetic, **eukaryotic,** and multicellular organisms.

planula The ciliated **larva** of **cnidarians** (Fig. 7.8).

plate tectonics The process involved in the movement of large plates on the earth's crust.

pleistocene A geological period, which began about 2 million years ago, characterized by a series of **ice ages.**

pleuston Organisms that live right at the sea surface, with part of the body projecting into the air. Compare **neuston.**

pneumatocyst A gas-filled bladder in **seaweeds** (Fig. 6.1).

pneumatophore Upward extension of roots of some **mangroves** (Fig. 12.19).

pod A **school** of **cetaceans.**

pogonophorans See **beard worms.**

poikilotherm An organism whose body temperature varies with that of its surroundings. Compare **homeotherm.**

polar easterlies Variable winds that blow at high latitudes (Fig. 3.18).

pollen The structure that produces the male **gamete** in **flowering plants.**

pollution The introduction of harmful substances or heat energy into the environment by humans.

polychaetes (class *Polychaeta*) **Segmented worms** that typically have **parapodia** (Figs. 7.16 and 7.17).

polychlorinated biphenyls (PCBs) A group of **chlorinated hydrocarbon** pollutants.

polymetallic nodules Lumps of minerals (including manganese, nickel, and other valuable minerals) that are found on the sea floor beyond the **continental shelf.**

polyp The cylindrical, typically attached stage of **cnidarians** (Figs. 7.6 and 14.2).

population A group of organisms belonging to the same **species** and living in the same place.

pore cell (porocyte) The tube-like cell of **sponges** that forms a pore, or *ostium* (pl. *ostia*).

practical salinity units (PSU) A measurement of seawater **salinity** based on electrical conductivity, numerically equivalent to parts per thousand.

precious corals **Gorgonians** that secrete a red or pink skeleton consisting of fused **calcareous spicules.**

predation The act of an animal, or *predator,* eating another organism, or *prey.* A *top predator* is one that feeds at the top of the **food chain.**

pressure The weight exerted over a unit area of surface. This is equal to 1 *atmosphere* (14.7 lb per square inch) at the sea surface and 1 atmosphere plus the pressure exerted by the **water column,** which is 1 atmosphere per 10 m (33 ft) of depth.

primary producer (producer) An **autotroph.** An organism that carries out **primary production.**

primary production The conversion of the inorganic carbon, usually in the form of **carbon dioxide,** into **organic compounds** by **autotrophs.**

primary productivity The rate of **primary production,** that is, the amount of carbon fixed under a square meter of sea surface in a day or in a year (Fig. 10.17).

proboscis An extension near the mouth that in some **invertebrates** helps in the capture or collection of food.

profile A graph that shows changes in temperature, salinity, or any other parameter with depth (Fig. 3.8).

prokaryote An organism, such as bacteria, with a **prokaryotic cell.**

prokaryotic cell The simplest type of cell, one that lacks a **nucleus** and most other kinds of **organelles** (Fig. 4.7). Compare **eukaryotic cell.**

protective coloration Coloration that benefits the individual by providing concealment from predators.

protein A large group of complex **nitrogen**-containing **organic molecules** that play many crucial roles in organisms.

protists Collection of different groups of relatively simple **eukaryotes,** including unicellular forms and multicellular algae. Formerly members of the kingdom *Protista* but now grouped together mostly for convenience.

protochordates **Chordates** that lack a backbone.

protozoans Animal-like **protists;** the various groups of unicellular, **eukaryotic protists** that are mostly heterotrophic.

pseudopodium A thin or blunt extension of the cytoplasm.

psychrophilic Cold-temperature-loving. Applied to organisms or enzymes that grow or function best, or only, at cold temperatures.

pteropods **Pelagic gastropods** in which the **foot** is modified for swimming and the shell is reduced or absent (Fig. 15.10).

pyloric caecum (pl. **caeca**) Each of the slender, blind tubes found in the intestines of many **bony fishes.**

pyramid of biomass The decrease in biomass that is observed in each higher level of a **food chain.**

pyramid of energy The decrease in energy that is observed in each higher level of a **food chain.**

pyramid of numbers The decrease in the number of individuals that is observed in each higher level of a **food chain.**

R

radial symmetry The regular arrangement of similar body parts around a central axis (Figs. 7.6 and 7.13*a*). Compare **bilateral symmetry.**

radioactivity The emission of *radiation* by unstable **atoms** in the form of particles and rays.

radiolarian ooze A type of **biogenous sediment** that consists mostly of the **silica** shells of **radiolarians.**

radiolarians (phylum *Polycystina*) **Protozoans** with a **silica** shell and **pseudopodia** (Fig. 5.11).

radula The ribbon-like band of teeth of **molluscs** (Figs. 7.20, 7.21, and 7.27).

recombination The formation of new genetic combinations, such as the one that takes place during **fertilization.**

recruitment The entry of young individuals into a **population** or, in fisheries biology, into a fished stock.

rectal gland A gland in the **cloaca** of **cartilaginous fishes** that excretes excess salts.

red algae (phylum *Rhodophyta*) **Seaweeds** that contain characteristic red pigments.

red clay A fine sediment that is the most common type of **lithogenous sediment** in the open ocean floor.

red tide An extensive **bloom** of **phytoplankton** that discolors the water.

reef crest The shallow outer edge of the **reef slope** of a **coral reef** (Fig. 14.15).

reef flat The wide and shallow upper surface of a **coral reef** (Fig. 14.15).

reef slope The outer, steep margin of a coral reef (Fig. 14.15). Also see **fore reef.**

refraction The change in the direction of a wave as it moves into shallow water (Figs. 11.8 and 11.9).

regeneration The ability of an organism to grow a body part that has been lost.

renewable resource A resource that is naturally replaced.

replication The copying of a cell's **deoxyribonucleic acid (DNA)** before the cell divides.

reproductive isolation The inability of separate **populations** to interbreed.

reproductive strategy The reproductive patterns that are followed by a particular species.

reptiles (class *Reptilia*) **Vertebrates** with scales on their skin and leathery eggs that are laid on land. Marine reptiles include *sea turtles, sea snakes,* the *marine iguana,* and the *saltwater crocodile.*

resource partitioning The sharing of resources by specialization.

respiration See **aerobic respiration.** In this text the term "respiration" by itself refers to aerobic respiration.

respiratory exchange See **gas exchange.**

respiratory tree The branched extensions of the posterior end of the digestive tract of **sea cucumbers** that are involved in **gas exchange.**

rete mirabile A network of blood vessels that in some fishes functions as a heat-exchange system to help keep the internal body temperature higher than that of the water (Fig. 15.22).

retroviruses **Viruses** that contain **RNA** instead of **DNA.**

ribbon (nemertean) worms (phylum *Nemertea*) **Invertebrates** with a complete digestive tract, a true circulatory system, and a long **proboscis** to capture prey (Fig. 7.15).

ribosomes **Organelles** where a cell's **proteins** are made.

rift A crack in the earth's crust formed as pieces of the crust separate.

RNA (ribonucleic acid) **Nucleic acids** that translate the genetic information contained in **DNA** (deoxyribonucleic acid) into **proteins** and that have many other functions in the cell.

rockweeds (wracks) Brown algae such as *Fucus* that inhabit rocky shores in temperate areas.

rorquals Blue, fin, and the other **baleen whales** that display long grooves on the underside (Figs. 9.15 and 9.18).

roundworms See **nematodes.**

S

salinity The total amount of **salts** dissolved in seawater. It is generally expressed in parts per thousand (‰).

salivary gland Any of the glands in **molluscs, vertebrates,** and other animals that release digestive **enzymes** into the mouth.

salmon ranching Practice in which cultured juvenile salmon are released into fresh water and allowed to migrate to sea so they can be harvested later when they return as adults.

salps (class *Thaliacea*) Pelagic **tunicates** with a transparent, cylindrical body, sometimes forming long colonies (Fig. 15.8).

salt A substance that consists of **ions** that have opposite electrical charges.

salt gland A gland that secretes excess salts in seabirds and sea turtles.

salt marsh A grassy area that extends along the shores of **estuaries** and sheltered coasts in temperate and subpolar regions.

salt wedge A layer of denser, saltier seawater that flows along the bottom in **estuaries** (Fig. 12.3).

sand dollars **Sea urchins** with a flat, round test and short spines that live partly buried in soft sediments (Fig. 7.47*b*).

Sargasso Sea The region of the Atlantic Ocean north of the West Indies that is characterized by floating masses of *Sargasso weed,* a **brown alga.**

scaphopods See **tusk shells.**

scavenger An animal that feeds on dead organic matter.

school A well-defined group of fishes or **cetaceans** of the same species. Also see **pod.**

scientific method The set of procedures by which scientists learn about the world (Fig. 1.20).

scleractinian corals **Anthozoans** with a solid **calcareous** skeleton that are the most important reef-building corals.

sclerosponges (coralline sponges) **Sponges** with a massive **calcareous** skeleton (Fig. 7.5*c*).

scuba (*s*elf-*c*ontained *u*nderwater *b*reathing *a*pparatus) Equipment that allows breathing underwater from tanks of compressed air.

scyphozoans (class *Scyphozoa*) **Cnidarians** whose life cycle includes a conspicuous **medusa** and a much reduced or absent **polyp.**

sea A **wave** that has a sharp peak and a relatively flat **wave trough.** Seas are found in areas where waves are generated by the wind (Fig. 3.29).

sea anemones **Anthozoans** that consist of one large **polyp.**

sea cows See **sirenians.**

sea cucumbers (class *Holothuroidea*) **Echinoderms** with a soft, elongate body that lacks spines.

sea-floor spreading The process by which new sea floor is formed as it moves away from *spreading centers* in **mid-ocean ridges.**

seagrasses Grass-like **flowering plants** such as *eelgrass* that are adapted to live at sea (Fig. 6.13).

sea lilies See **crinoids.**

seamount A submarine volcano in the **abyssal plain.**

sea slugs See **nudibranchs.**

sea spiders (class *Pycnogonida*) **Arthropods** that have a reduced body and four pairs of legs (Fig. 7.41).

sea squirts (**ascidians;** class *Ascidiacea*) **Tunicates** with a typically sac-like, attached body as adults (Figs. 7.51*a* and 7.52).

sea stars (**starfishes;** class *Asteroidea*) **Echinoderms** with five or more radiating arms and **tube feet** that are used in locomotion.

sea urchins (class *Echinoidea*) **Echinoderms** with a round or flattened test and movable spines.

seaweeds (macrophytes) Large, multicellular **algae.**

sediment Loose material such as sand and mud that settles on the bottom. Also see **biogenous** and **lithogenous sediments.**

seeding In **mariculture,** the release of cultured juvenile individuals to enrich a natural **stock.**

segmentation The division of the body into similar compartments, or *segments.*

segmented worms (**annelids;** phylum *Annelida*) **Invertebrates** that display an elongate body with distinct **segmentation** and a digestive tract that lies in a **coelom.**

seismic sea waves See **tsunami.**

self-regulating population A **population** with a growth rate that is dependent on its own numbers.

self-shading Reduction in the amount of light available to **phytoplankton** that live below other phytoplankton.

semidiurnal tide A tidal pattern with two high and two low **tides** each day (Fig. 3.34*a*).

septa The thin tissue partitions in the **polyp** of **anthozoans.**

sequence (of nucleic acids) The order in which *nucleotides* occur on a **nucleic acid** molecule, which specifies the information contained in the molecule.

sessile An organism that lives attached to the bottom or to a surface.

seta (pl. **setae**) The bristles of **polychaetes.**

sex hormone A **hormone** that controls the timing of reproduction and sexual characteristics in **vertebrates.**

sexual reproduction Reproduction that involves the union of **gametes.** Compare **asexual reproduction.**

shear boundary The boundary between two plates that move past each other on the earth's surface. Also see **fault.**

shelf break The section of the **continental shelf** where the slope abruptly becomes steeper, usually at a depth of 120 to 200 m (400 to 600 ft) (Figs. 2.19 and 2.20).

silica (SiO_2) A mineral similar to glass that is the major component of the cell wall, shell, or skeleton of many marine organisms.

siliceous Made of **silica.**

siliceous ooze A type of **biogenous sediment** that consists mostly of the **silica** shell and skeletons of marine organisms. Also see **diatomaceous ooze** and **radiolarian ooze.**

silicoflagellates (phylum *Heterokontophyta,* class *Chrysophyta*) Unicellular and **eukaryotic** members of the **phytoplankton** that have a star-shaped **silica** skeleton (Fig. 5.9).

simple sugar A sugar, such as **glucose,** that cannot be broken down into simpler sugar molecules.

siphon (funnel) The tube-like extension through which water flows in and out of the **mantle cavity** in **bivalves** and **cephalopods,** and in **tunicates.**

siphonophores **Hydrozoans** that exist as drifting colonies.

sipunculans See **peanut worms.**

sirenians (**sea cows;** order *Sirenia*) Marine **mammals** with anterior flippers, no rear limbs, and a paddle-shaped tail (Fig. 9.13).

sludge Concentrated wastes extracted from sewage during sewage treatment.

soft corals (order *Alcyonacea*) Colonial **anthozoans** with no hard skeleton.

solute Any material dissolved in a *solvent.*

sonar (*s*ound *n*avigation *r*anging) A technique or equipment used to locate objects underwater by the detection of echoes (Fig. 1.7).

Southern Oscillation See **El Niño—Southern Oscillation.**

spawning The release of **gametes** or eggs into the water.

species Individuals of the same kind that cannot breed with those belonging to other kinds.

spermaceti organ The **melon** of sperm whales. It contains *spermaceti,* an oil once widely used in candle making.

spermatophore A packet of sperm in **cephalopods.**

spicule Any of the small **calcareous** or **siliceous** bodies embedded among the cells of **sponges** or in the tissues of other **invertebrates.**

spiracle One of two openings behind the eyes of **cartilaginous fishes.**

spiral valve A spiral portion in the intestine of **cartilaginous fishes.**

sponges (phylum *Porifera*) **Invertebrates** that consist of a complex aggregation of cells, including **collar cells,** and have a skeleton of fibers and/or **spicules.**

spongin The resistant fibers of **sponges.**

spore The **asexual,** sometimes resistant structure produced by some **algae.** Also see **zoospore.**

sporophyte The **diploid, spore**-producing generation in many **seaweeds.** Compare **gametophyte.**

spout (blow) The water vapor and seawater that is observed when whales surface and exhale.

spring tides The **tides** with a large **tidal range;** they occur around the times of full or new moon. Compare **neap tides.**

standing stock (standing crop) The total amount, or **biomass,** of an organism at a given time.

starch A **carbohydrate** that consists of chains of **simple sugars.**

statocyst A fluid-filled cavity provided with sensitive hairs and a small free body that is used to orient animals with respect to gravity.

stenohaline Organism that can tolerate a narrow range of salinities. Compare **euryhaline.**

stipe The stem-like portion of the **thallus** of **seaweeds** (Fig. 6.1).

stock The size of a **population.**

stratification The separation of the **water column** into layers, with the densest water at the bottom and the least dense at the surface (Fig. 3.22). A stratified water column is said to be *stable.* An *unstable* column results when the surface water becomes more dense than the water below.

stromatolites Massive **calcareous** skeletons formed by **cyanobacteria** (Fig. 5.4).

structural color A color that results when light is reflected by a particular surface.

structural molecule A molecule, such as **cellulose,** that provides support and protection.

subduction The downward movement of a plate into the mantle that occurs in **trenches,** which are also known as *subduction zones.*

sublittoral zone See **subtidal zone.**

submarine canyon A narrow, deep depression in the **continental shelf** formed by the erosion of rivers or glaciers before the shelf was submerged (Fig. 2.20).

subsidence The sinking of a landmass.

substrate The type of bottom or material on or in which an organism lives.

subtidal zone The bottom above the **continental shelf** (Fig. 10.12).

succession See **ecological succession.**

succulent A fleshy plant that accumulates water.

sulfide One of the minerals that is abundant in the hot water that seeps through **hydrothermal vents.**

surf A **wave** that becomes so high and steep as it approaches the shoreline that it breaks.

surface (mixed) layer The upper layer of water that is mixed by wind, waves, and currents (Fig. 3.24).

surface-to-volume ratio (S/V ratio) The amount of surface area relative to the total volume of an organism (Fig. 4.17).

suspension feeder An animal that feeds on particles suspended in the water (Fig. 7.3). Compare **deposit feeder, filter feeder.**

swarming The aggregation of individuals for **spawning** or other purposes.

sweeper tentacle A type of **tentacle** in corals that is used to sting neighboring colonies.

swell A **wave** with a flatter, rounded **wave crest** and **trough.** Swells are found away from the area where waves are generated by the wind (Fig. 3.29).

swim bladder The gas-filled sac in the body cavity of **bony fishes** that is involved in the adjustment of buoyancy (Fig. 8.12).

symbiosis A close relationship between two species, including **commensalism, mutualism,** and **parasitism.**

system (organ system) A group of **organs** specialized for one function.

T

tadpole larva The larva of **tunicates.**

tapeworms Parasitic **flatworms,** typically consisting of a chain of repeated units.

taste buds Structures in the mouth and other locations of fishes that are sensitive to chemical stimuli.

taxon (pl. **taxa**) A group of organisms that share a common ancestry.

tectonic estuary An **estuary** that results from the sinking of land due to movements of the **crust.**

tentacle A flexible, elongate appendage.

territory A home area that is defended by an animal.

Tethys Sea A shallow sea that once separated the Eurasian and African sections of the supercontinent **Pangaea.** It eventually gave rise to the modern Mediterranean Sea (Figs. 2.16*a* and 2.16*b*).

tetrapods **Vertebrates** that have two pairs of legs, a group that includes the **cetaceans.**

thallus The complete body of a **seaweed.**

theory A **hypothesis** that is accepted as "true" for the time being because it has passed test after test and is supported by a large body of evidence.

thermal pollution Pollution by heated water.

thermocline A zone in the **water column** that shows a sudden change in temperature with depth. The *main thermocline* is the zone where the temperature change marks the transition between the warm surface water and the cold deep water (Figs. 3.8 and 3.22).

thermohaline circulation Ocean circulation that is driven by differences in water density, due to variations in water temperature and salinity, rather than by the wind or tides.

threatened species A species that occurs in unnaturally low numbers.

tidal bore A steep wave generated as high tides move up some estuaries and rivers.

tidal current A **current** that is generated by **tides.**

tidal energy **Energy** that can be harnessed as a result of the movement of **tides.**

tidal marsh See **salt marsh.**

tidal range The difference in water level between successive high and low **tides.**

tide The periodic, rhythmic rise and fall of the sea surface.

tide pool A depression that holds seawater at low tide.

tide table A table that gives the predicted time and height of **tides** for particular points along a coast.

tintinnids **Ciliates** that secrete vase-like cases, or *loricas* (Fig. 5.13).

tissue A group of cells specialized for one function.

tortoiseshell The polished shell of hawksbill turtles.

trade winds Steady winds that blow from east to west toward the Equator, replacing the hot air that rises at the Equator (Fig. 3.18).

transform fault A large horizontal displacement in the mid-ocean ridge.

transplantation The intentional introduction of a species.

trematodes See **flukes.**

trench A narrow, deep depression in the sea floor (Figs. 2.11 and 2.12).

trochophore A planktonic **larva** found in **polychaetes,** some **molluscs,** and other **invertebrates** (Fig. 15.11*d*).

trophic level Each of the steps in a **food chain.**

trophic pyramid The pyramid-like relationship found in the **pyramids of biomass, energy,** and **numbers** of organisms in a **food chain.**

tsunami (seismic sea waves) Long, fast waves produced by earthquakes and other seismic disturbances of the sea floor.

tube foot Any of the external muscular extensions of the **water vascular system** of **echinoderms.**

tubular eyes Specialized eyes of many **midwater** animals that allow acute upward or downward vision.

tunic The outer covering of **sea squirts** (Fig. 7.52*b*).

tunicates (subphylum *Urochordata*) **Chordates** that show the three basic chordate characteristics only in the larva.

turbellarians Mostly free-living **flatworms** (Fig. 7.14).

tusk shells (**scaphopods;** class *Scaphopoda*) **Molluscs** that have an elongate, tapered shell that is open at both ends.

U

umbo The region around the hinge of a bivalve's shell (Fig. 7.23).

upwelling The process by which colder water rich in **nutrients** rises from a lower to a higher depth. It includes *coastal* and *equatorial upwelling* (Figs. 15.30 to 15.33).

urea A toxic waste product of some vertebrates.

urogenital opening The common opening for urine and **gametes** in **bony fishes** and other animals.

uterus (womb) The portion of female mammals' reproductive tract in which the **embryo** develops.

V

valve Any of the two shells of **bivalves** and **lamp shells.**

vegetative reproduction See **asexual reproduction.**

veliger A planktonic **larva** in **gastropods** and **bivalves** (Fig. 15.11*a*).

ventral The underside or belly surface of an animal with **bilateral symmetry** (Fig. 7.13*b*).

vertebra (pl. **vertebrae**) Each of the bones that make up the backbone.

vertebrates (subphylum *Vertebrata*) **Chordates** with a backbone.

vestigial Undeveloped structure that is fully developed in ancestral species.

vestimentiferans **Pogonophorans** that are common at **hydrothermal vents** (Fig. 16.29).

viruses Non-cellular particles containing **nucleic acid** but unable to reproduce unless infecting living cells.

viviparous An animal whose eggs develop inside the female while the **embryo** derives nutrition from the mother.

W

warning coloration Coloration that allows organisms to escape from predators by advertising something harmful or distasteful.

water column The vertical column of seawater that extends from the surface to the bottom.

water mass A body of water that can be identified by its temperature and salinity.

water vascular system A network of water-filled canals in **echinoderms** used in locomotion and food-gathering (Figs. 7.44 and 7.48).

wave The undulation that forms as a disturbance moves along the surface of the water. Waves can be described by their *height* (the vertical distance between **wave crest** and **trough**), *wavelength* (the horizontal distance between adjacent **crests**), and *period* (the time the wave takes to move past a given point) (Fig. 3.26).

wave crest The highest part of a **wave** (Fig. 3.26).

wave shock The intensity of the impact of a **wave.**

wave trough The lowest part of a **wave** (Fig. 3.26).

weathering The physical and chemical breakdown of rocks.

westerlies The winds that blow from west to east at middle latitudes (Fig. 3.18).

wetlands Areas flooded by tides or with visible standing water such as **salt marshes, mangrove forests,** and freshwater marshes.

world ocean A concept that is used to indicate that all oceans on earth are interconnected.

Y

yolk sac A yolk-containing sac that is attached to the **embryo** of *fishes* and other **vertebrates.**

Z

zonation The presence of organisms within a particular range, as in the *vertical zonation* observed in the **intertidal.**

zooid Each member of a colony of **bryozoans** and other colonial **invertebrates.**

zooplankton The **heterotrophic,** animal and protozoan component of **plankton.** Compare **phytoplankton.**

zoospore A **spore** provided with one or more **flagella.**

zooxanthellae **Dinoflagellates** that live within the tissues of reef corals and other marine animals (Fig. 14.1).

zygote The **diploid** cell that results from **fertilization,** that is, a fertilized egg.

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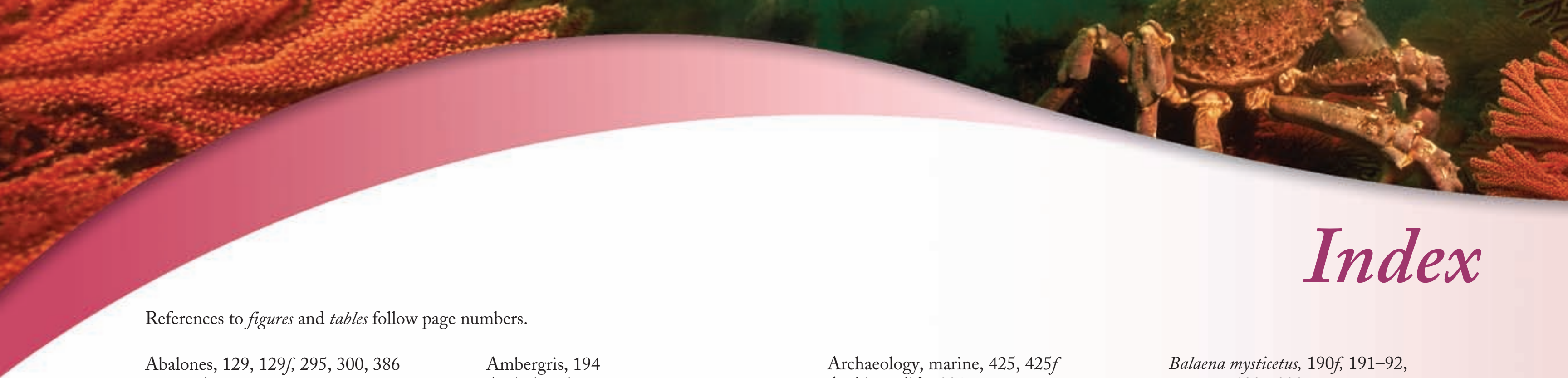

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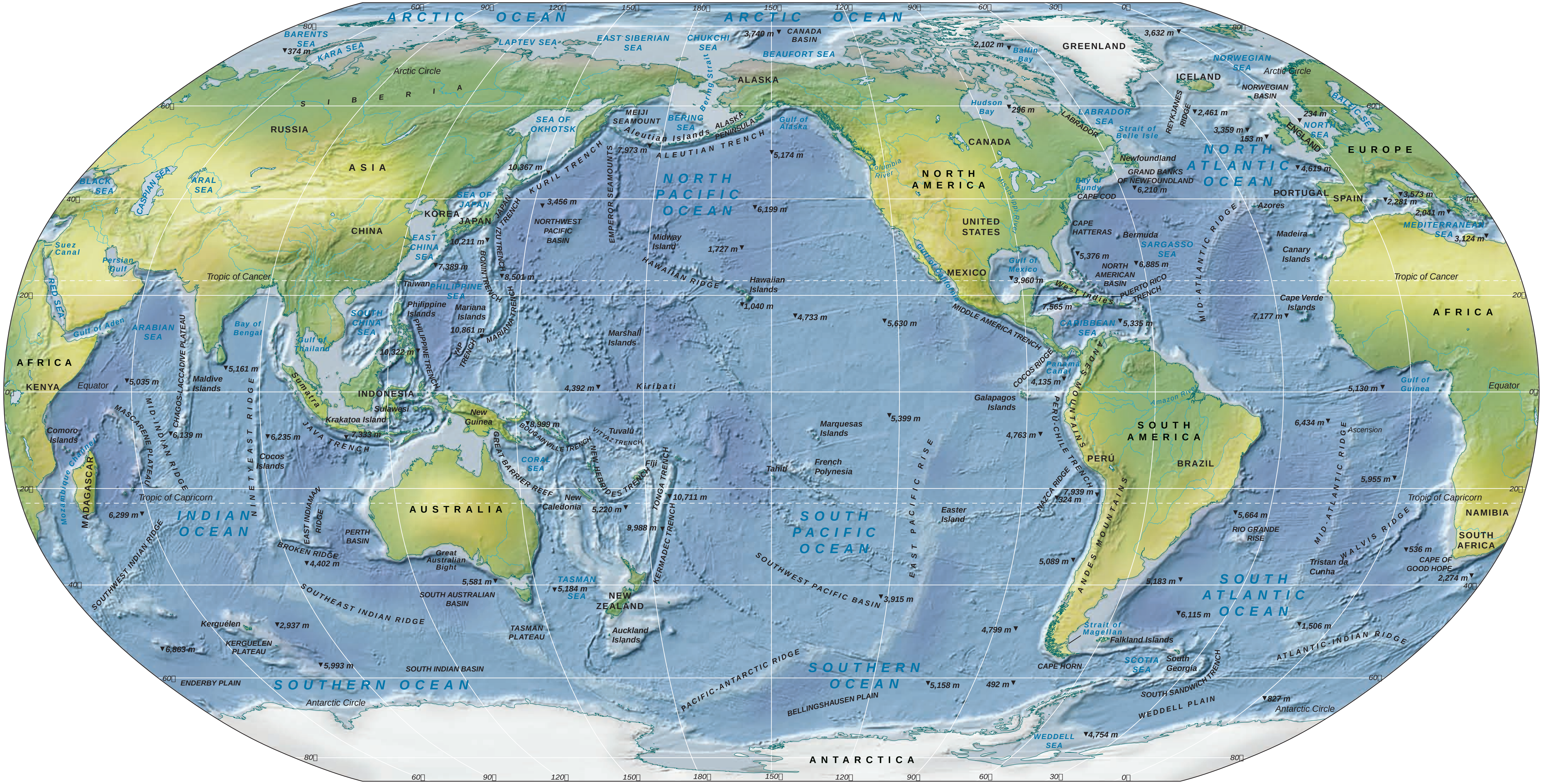
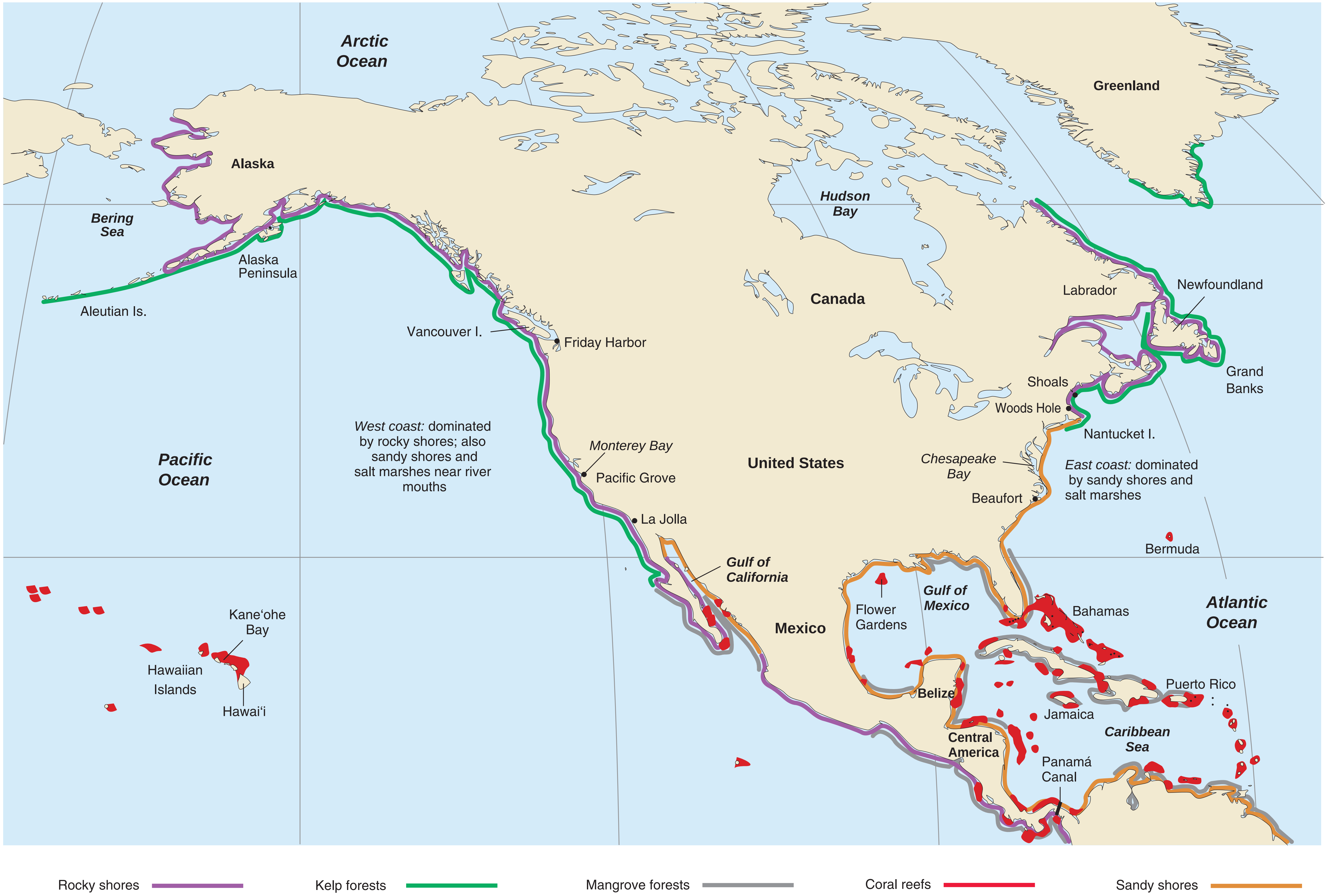
The World Ocean


ARCTIC OCEAN
BARENTS SEA
374 m
KARA SEA
LAPTEV SEA
EAST SIBERIAN SEA
CHUKCHI SEA
3,740 m
CANADA BASIN
BEAUFORT SEA
2,102 m
Baffin Bay
GREENLAND
3,632 m
NORWEGIAN SEA
Arctic Circle
ICELAND
NORWEGIAN BASIN
REYKJANES RIDGE
2,461 m
3,359 m
153 m
234 m
NORTH SEA
BALTIC SEA
ENGLAND
EUROPE
S I B E R I A
RUSSIA
ASIA
BLACK SEA
CASPIAN SEA
ARAL SEA
SEA OF OKHOTSK
Bering Strait
ALASKA
Gulf of Alaska
MEIJI SEAMOUNT
BERING SEA
Aleutian Islands
ALASKA PENINSULA
ALEUTIAN TRENCH
7,973 m
5,174 m
10,367 m
KURIL TRENCH
SEA OF JAPAN
KOREA
JAPAN
JAPAN TRENCH
IZU TRENCH
BONIN TRENCH
3,456 m
NORTHWEST PACIFIC BASIN
EMPEROR SEAMOUNTS
NORTH PACIFIC OCEAN
6,199 m
Midway Island
1,727 m
HAWAIIAN RIDGE
Hawaiian Islands
1,040 m
4,733 m
5,630 m
CHINA
EAST CHINA SEA
10,211 m
7,389 m
8,501 m
Taiwan
PHILIPPINE SEA
Philippine Islands
Mariana Islands
MARIANA TRENCH
10,861 m
YAP TRENCH
10,322 m
PHILIPPINE TRENCH
SOUTH CHINA SEA
Gulf of Thailand
Bay of Bengal
ARABIAN SEA
Persian Gulf
Suez Canal
RED SEA
Gulf of Aden
Tropic of Cancer
Marshall Islands
Kiribati
4,392 m
HUDSON Bay
296 m
LABRADOR SEA
LABRADOR
Strait of Belle Isle
CANADA
Columbia River
NORTH AMERICA
Mississippi River
Bay of Fundy
Newfoundland
GRAND BANKS OF NEWFOUNDLAND
6,210 m
CAPE COD
NORTH ATLANTIC OCEAN
4,619 m
UNITED STATES
CAPE HATTERAS
Bermuda
SARGASSO SEA
PORTUGAL
SPAIN
Azores
3,573 m
2,281 m
2,041 m
MEDITERRANEAN SEA
3,124 m
Madeira
Canary Islands
Gulf of California
MEXICO
Gulf of Mexico
3,960 m
5,376 m
6,885 m
NORTH AMERICAN BASIN
PUERTO RICO TRENCH
West Indies
7,565 m
MIDDLE AMERICA TRENCH
CARIBBEAN SEA
5,335 m
MID-ATLANTIC RIDGE
Cape Verde Islands
7,177 m
AFRICA
Panama Canal
COCOS RIDGE
4,135 m
ANDES MOUNTAINS
Galapagos Islands
Amazon River
Equator
5,130 m
Gulf of Guinea
KENYA
5,035 m
Maldive Islands
CHAGOS-LACCADIVE PLATEAU
5,161 m
MID-INDIAN RIDGE
MASCARENE PLATEAU
Comoro Islands
Mozambique Channel
MADAGASCAR
6,139 m
NINETYEAST RIDGE
INDONESIA
Sumatra
Sulawesi
Krakatoa Island
JAVA TRENCH
7,333 m
6,235 m
Cocos Islands
New Guinea
8,999 m
BOUGAINVILLE TRENCH
Tuvalu
VITYAZ TRENCH
NEW HEBRIDES TRENCH
Fiji
TONGA TRENCH
10,711 m
GREAT BARRIER REEF
CORAL SEA
Marquesas Islands
5,399 m
French Polynesia
Tahiti
EAST PACIFIC RISE
4,763 m
PERU-CHILE TRENCH
PERÚ
SOUTH AMERICA
BRAZIL
6,434 m
Ascension
5,955 m
Tropic of Capricorn
6,299 m
INDIAN OCEAN
EAST INDIAMAN RIDGE
AUSTRALIA
New Caledonia
5,220 m
9,988 m
KERMADEC TRENCH
SOUTH PACIFIC OCEAN
Easter Island
NAZCA RIDGE
7,939 m
324 m
5,664 m
RIO GRANDE RISE
NAMIBIA
WALVIS RIDGE
SOUTH AFRICA
536 m
CAPE OF GOOD HOPE
2,274 m
PERTH BASIN
BROKEN RIDGE
4,402 m
Great Australian Bight
SOUTHWEST INDIAN RIDGE
SOUTHWEST PACIFIC BASIN
5,089 m
Tristan da Cunha
5,581 m
TASMAN SEA
5,184 m
NEW ZEALAND
SOUTH AUSTRALIAN BASIN
SOUTHEAST INDIAN RIDGE
3,915 m
5,183 m
SOUTH ATLANTIC OCEAN
6,115 m
1,506 m
Kerguélen
2,937 m
KERGUELEN PLATEAU
6,863 m
TASMAN PLATEAU
Auckland Islands
4,799 m
Strait of Magellan
Falkland Islands
ATLANTIC-INDIAN RIDGE
5,993 m
SOUTH INDIAN BASIN
PACIFIC-ANTARCTIC RIDGE
CAPE HORN
SCOTIA SEA
South Georgia
SOUTH SANDWICH TRENCH
ENDERBY PLAIN
SOUTHERN OCEAN
5,158 m
492 m
827 m
Antarctic Circle
BELLINGSHAUSEN PLAIN
WEDDELL PLAIN
WEDDELL SEA
4,754 m
ANTARCTICA
80°
60°
40°
20°
0°
20°
40°
60°
80°
60°
90°
120°
150°
180°
150°
120°
90°
60°
30°
0°

Major Coastal Communities of North America


Arctic Ocean
Greenland
Alaska
Hudson Bay
Bering Sea
Alaska Peninsula
Aleutian Is.
Canada
Labrador
Newfoundland
Vancouver I.
Friday Harbor
Grand Banks
Shoals
Woods Hole
Nantucket I.
West coast: dominated by rocky shores; also sandy shores and salt marshes near river mouths
Monterey Bay
Pacific Grove
United States
Chesapeake Bay
East coast: dominated by sandy shores and salt marshes
Beaufort
Pacific Ocean
La Jolla
Bermuda
Gulf of California
Gulf of Mexico
Flower Gardens
Mexico
Bahamas
Atlantic Ocean
Kane'ohe Bay
Hawaiian Islands
Hawai'i
Belize
Puerto Rico
Jamaica
Central America
Caribbean Sea
Panamá Canal
Rocky shores
Kelp forests
Mangrove forests
Coral reefs
Sandy shores

About the Cover

Lionfishes are among the most spectacular of coral reef fishes, but the long, feathery fins are not just for show. Hunting at night, the lionfish uses the fins to herd shrimps, crabs, and small fishes into a corner before snapping them up. Like other members of the scorpionfish family, the lionfish has highly venomous spines in the dorsal and anal fins along its midline—a jab can be excruciating or even fatal. The devil firefish occurs in the eastern Mediterranean, Red Sea, and western Indian Ocean. In the eastern Indian and Tropical Pacific oceans it is replaced by the very similar red lionfish *(Pterois volitans)*. Both species have been introduced into the Atlantic Ocean along the coast of North America by the rupture of a seaside aquarium during Hurricane Andrew in 1992 and probably also through deliberate releases by aquarium hobbyists. With no known natural predators, these lionfishes rapidly established viable populations in the waters off the southeastern United States, where they now outnumber many native fish species. They have been observed as far north as Long Island, New York, although cold winter water temperatures will probably prevent them from becoming established there. Lionfishes have also been observed in the Gulf of Mexico, Bermuda, and the Bahamas, and could spread throughout the Caribbean and possibly even beyond. How far they will spread, and how they might affect populations of native fish species, is not known.

Cover photo: A devil firefish *(Pterois muricta)*, also known as the Indian lionfish, from the Red Sea.

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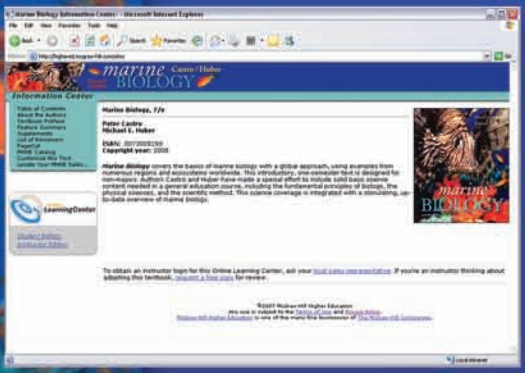

Marine Biology, 7/e

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